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Greetings from London

E. E. W.

June 1931

THE ORIGIN OF THE HUMAN SKELETON

THE ORIGIN OF THE HUMAN SKELETON

AN INTRODUCTION TO HUMAN OSTEOLOGY

BY

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LONDON

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PREFACE

FIFTY years ago the great English anatomist Owen suggested that among the fossil mammal-like reptiles of South Africa were possibly to be found the ancestors of mammals. Huxley and others opposed this view; but towards the end of the nineteenth century Osborn again strongly advocated the opinion that the cynodonts, or higher mammal-like reptiles, approach the mammals so closely in many characters as to suggest that if the mammalian ancestor was not a cynodont the cynodonts were at least nearly allied to the ancestors.

In the same year as Osborn's first paper on the subject appeared (1897) I came out to South Africa to make a fuller study of the Karroo reptiles on the spot, and to try if possible to solve the question of the origin of mammals. As the result of my thirty-odd years' work I have been successful not only in greatly adding to our knowledge of the mammal-like reptiles, but, I think, in definitely solving the question of the mammalian origin. The work has also enabled us to solve the problem of the origin of lizards and crocodiles, and to throw some new light on the origin of dinosaurs and birds.

For the last two years I have been engaged, with

the assistance of a grant from the Carnegie Trust, on a monograph on the mammal-like reptiles, which will bring together most of the results of my thirty years' work. But it has been suggested to me that a shorter book, dealing mainly with the origin of mammals from the anatomical point of view, would be useful to students. And as a knowledge of the structure of the mammalian ancestors throws light on many of the obscure problems of even human anatomy, I have collected the main results of palæontology which bear on the structure of the mammals in a form which I trust will be appreciated by anatomy students.

The study of human anatomy usually begins with the study of the bones, and though the detailed knowledge of the facts is of extreme importance the subject is rather a dull one. When, however, we begin to realize how the various structures have arisen, even the dead bones begin to live. We become, as it were, spectators of the steps by which man has been created, and, it may be, catch glimpses of the mysteries of the universe.

R. B.

GRAHAMSTOWN, SOUTH AFRICA,
27*th July* 1930.

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CHAPTER I

THE MAIN LINES OF VERTEBRATE EVOLUTION

In most animals and plants, and even in many of the unicellular, some firm structure is necessary to give support to the softer parts. In the higher animals, where striped muscle is developed for voluntary movement, it has been found by nature to be a great advantage to have a skeleton, which serves the double purpose of protecting and supporting the delicate internal organs, and also of giving attachment to the voluntary muscles.

Though in the animal kingdom we have a large variety of types of skeleton, many of them quite independently developed, we need not consider any of these except that which we find in the vertebrates, or backboned animals, as their type of skeleton has certainly been developed quite independently of that formed in any of the invertebrates.

The vertebrates form a group so well marked off from the invertebrates that it is a little difficult to be quite certain from which invertebrate group they have arisen.

The Ascidians, or sea-squirts, though unlike vertebrates when adult, have a free-swimming

larva which has a true notochord, and there can be no reasonable doubt that they are allied to the ancestors of the vertebrates.

Balanoglossus and *Ptychodera*, and other worm-like animals that are grouped under the order Enteropneusta, are also pretty clearly related, if more distantly, to the most primitive vertebrate, *Amphioxus*, and may be regarded as very specialised offshoots of the pre-vertebrate stock.

Cephalodiscus and *Rhabdopleura* are Polyzoa-like forms which also show a number of proto-vertebrate characters, and may represent specialised side branches from the same pre-vertebrate line as *Balanoglossus*, but further back.

The Echinoderms, though extremely specialised, and in their adult condition so unlike vertebrates that hardly any parts can be regarded as homologous, pass through a stage in their early development which suggests that, not improbably, the ancestral proto-Echinoderm was related to the early proto-vertebrate.

But there is scarcely a single invertebrate group for which the claim has not been made by some zoologist that it gave rise to the vertebrates.

Although, however, there is thus great doubt concerning their ancestors, we can trace the later evolution of the vertebrates with almost perfect confidence; and, before discussing in detail the

evolution of each of the principal bones of the skeleton, it will be well to review the different steps in the evolution of the animals themselves, from the earliest vertebrates to man, not only to note how the skeleton has been formed, but how the changes in habit have resulted in the changes in the bones.

The earliest vertebrates probably lived mainly embedded in mud, and had no more skeleton than an *Amphioxus*. Doubtless there was a firm notochord, whose sheath gave attachment to the muscle segments, but the skin was unprotected. Of such early forms, of course, palæontology has no knowledge—there was nothing that could be preserved as fossils.

But so far back as in Silurian times we find primitive fishes that had developed an early exoskeleton of small bony scales in the skin. These are probably allied to the lampreys and hagfishes of to-day, and side branches from the main line which led to the higher vertebrates. We know very little of their structure, and they are mainly of interest in showing that at a very early stage fishes developed fine osseous scales in the skin. It is, however, in the sharks that we get the first clearly defined stage in the evolution of the higher forms. For not only have we many fossil sharks of great interest, but a large number of types have survived till to-day, and we can study not only all

details of the adult structure, but also the embryonic condition.

The study of the sharks reveals to us not only how the exoskeleton originated but how the internal arose, and also how the limbs originated.

In the sharks we find an internal skeleton of cartilaginous elements and an exoskeleton of minute bony scales. The internal skeleton has a cartilaginous skull, made up of nasal and auditory capsules; a support and protection for the brain with connecting bars of cartilage and cartilages for the support of the jaws and gills. The notochord and spinal cord have developed along them a series of cartilaginous elements, mainly for the attachment of the body muscles, and a series of cartilages are developed for the support of the fins.

Very early in the evolution of fishes there were doubtless developed a dorsal and a ventral fin, which assisted the animals in swimming by lateral movements. Later on some fishes, through living mostly on the sand and mud at the sea-bottom, began to swim about mainly by an up-and-down movement of the body, and lateral fins developed, in exactly the same way as the dorsal and ventral fins had originated by lateral movements.

The ground-swimming habit, while it resulted in the development of lateral fins, converted the dorsal and ventral fins into anterior and posterior dorsals,

FIG. 1.—*A*. Outline restoration of the primitive shark *Cladoselache*. Mainly after Dean.
B. Outline restoration of the lobe-finned fish *Eusthenopteron*. Mainly after Whiteaves.

a tail, and a ventral fin. Very soon some bottom-frequenting fishes again reverted to swimming in the upper water, and the lateral fins became divided into anterior and posterior portions. From these anterior and posterior lateral fins are descended the limbs of the higher vertebrates.[1]

The small bony scales that protect the skin of the sharks are found in some types to become enlarged and specialised round the jaws, and make it practically certain that the teeth are really only specialised scales.

From the sharks were developed the various types of bony fishes—the ganoids, the lobe-finned fishes and the lung-fishes; but the step from the cartilaginous sharks to the bony fishes is a large one, and one on which, as it took place in early Devonian times, palæontology throws little light. We can, however, easily imagine the changes that took place.

The great advances in evolution seem always to have been associated with changes in environment which resulted in changes of habits. All the ganoids, lung-fishes and lobe-finned fishes we know from the Lower Devonian appear to have been fresh-water

[1] By some zoologists it has been maintained that limbs arose from gill arches; and while it must be admitted that palæontology gives us too few facts to settle the question, the mode of development of the fins in sharks seems to the writer strongly to support the lateral-fin theory. The fins in the fossil shark *Cladoselache* also seem to suggest that they are portions of a once continuous lateral fin.

forms. And though possibly all three groups arose independently from shark ancestors, all agree in having had the minute bony shagreen of the shark altered into large bony scales; in having had large specialised bony scales developed to protect and strengthen the skull and jaws; and in having had much of the internal skeleton converted into real bone.

The ganoids gave rise to the bony fishes of to-day, and as they are quite off the line that led to the higher vertebrates they need not further concern us. Nor do the lung-fishes seem to have had any further important developments; the three living lung-fishes of to-day—the *Ceratodus* of Australia, the *Lepidosiren* of South America, and the *Protopterus* of Africa—have rather degenerated than advanced from the lung-fishes of Devonian times.

The lobe-finned fishes, or Rhipidistians, are however a group of great importance, and it is doubtless from one of them that the four-footed land-animals arose.

Osteolepis is the best known of the Devonian lobe-finned fishes, and it is probably not far from the form from which the higher vertebrates sprang.

Unfortunately, though the outer skull-bones are well known, very little is known of the internal elements, or even whether they were fully ossified. Other lobe-finned fishes however — especially the

American Upper Devonian forms, *Sauripterus* and *Eusthenopteron*—give us most interesting light on the internal structure.

Various opinions have been expressed as to how the fish's fin became a walking limb. Most have held that the whole fin became converted into a walking limb. But this, it appears to the writer, would have resulted in countless generations having had neither a good fin nor a good limb. In the Gurnard of to-day we see the front portion of the pectoral fin converted into crawling fingers, while the greater part remains still a good swimming fin. And the structure of the fin in *Sauripterus* suggests, as will be shown later, that in one of the Rhipidistians the front of the fin developed into a crawling limb while the back part of the fin still continued as a good swimming organ.

This Rhipidistian, which developed walking limbs out of the front parts of its lateral fins while still living in the water, probably also, like the lung-fishes, developed lungs long before any of its descendants went much on land.

The more primitive amphibians of to-day are almost entirely aquatic, and probably most of the early known forms lived mainly in the water. Too little is, however, known of the structure of the early amphibia to enable us to say with any confidence through which group the line passed that led to

FIG. 2.—Restoration of a primitive Carboniferous amphibian *Diplovertebron*. Slightly enlarged.

the reptiles. Most of the well-known labyrinthodonts seem to the writer to be too specialised to have been in the direct line, and the reptilian ancestors are more probably to be found in some of the little-known small forms. *Scincosaurus* is a small newt-like form, which has a tarsus so like what we should expect in the ancestor of the reptile as to suggest that it may be related to the reptilian ancestor; while *Gymnarthrus*, unfortunately known only by the skull, is evidently a small amphibian nearly related to the primitive reptiles. But at present we have no certain evidence of how the reptiles arose from the amphibians.

The most primitive true reptiles [1] that are adequately known are the small American genera, *Pantylus*, *Captorhinus*, and *Labidosaurus*, and these belong to an order some member of which was probably the common ancestor of all living higher vertebrates. These earlier reptiles are placed in a super-order called the *Anapsida*.

From this primitive reptilian order there have been at least two main lines of descent. One of

[1] By Watson, Romer, and some others, *Conodectes* (*Seymouria*) is held to be the most primitive known reptile. But Susskin supports the present writer in believing that *Conodectes* is really an amphibian which by a parallel development has come in a few characters to resemble reptiles. The fact that, though the skeleton is pretty fully known, there is this difference of opinion shows how hard it is to decide where to draw the line between a higher amphibian and a primitive reptile when we have only bones to judge by.

FIG. 3.—Restoration of a primitive Anapsid reptile *Captorhinus*. About half natural size.

these gave rise to the lizards, crocodiles, dinosaurs, and almost all the reptiles of Mesozoic times, and ultimately led to the birds. The other, with which alone we have at present to deal, led to the mammal-like reptiles, and then to the mammals, and finally to man.

The earliest members of the mammal-like reptiles probably differed little in outward appearance from the more primitive *Anapsida*. They were essentially lizard-like, though more clumsily built than most lizards. But soon the mammal-like reptiles began to be less lizard-like, through the development of more powerful limbs. Not improbably this first great step towards the mammals took place in the Permian swamps of South Africa, when the reptiles no longer ran over hard sandy ground but had to pick their steps among the *Glossopteris* fronds. And this walking with the body kept well above the ground gave rise to many changes in structure, as we shall see later.

There are many orders and sub-orders of the mammal-like reptiles, and they form a group almost as varied as the mammals themselves, but we need consider only those that are on or near the line of mammalian descent.

It is extremely fortunate for the student of the ancestors of the mammals that we have in South Africa an almost continuous series of fossiliferous

rocks from the Middle Permian to the base of the Jurassic; which means that we have a fairly satisfactory record of the world's life-history from the year, say, 220,000,000 B.C. to possibly 150,000,000 B.C.

By far the commonest of the mammal-like reptiles found in the Permian and Triassic shales of South Africa is an animal called *Dicynodon*, from the fact that in the males there are two tusk-like canines. There are, however, no other teeth, and the front of the beak had a tortoise-like horny sheath. Animals of this and allied genera vary in size from forms smaller than rats to others as large as tapirs. Though the Dicynodonts—or Anomodonts, as they are called—have such peculiarly specialised beaks, and died out in Triassic times leaving no descendants, they are very interesting in having many mammal-like characters, some of which are doubtless due to a parallel development. Thus both the shoulder girdle and the pelvis, as we shall see later, are essentially mammalian in structure, and in both the hand and foot there is already the mammalian digital formula of 2,3,3,3,3.

Associated with the Anomodonts in Upper Permian times are two sub-orders of carnivorous mammal-like reptiles, which doubtless preyed on the herbivorous Dicynodonts. These are the Gorgonopsia and the Therocephalia. They resemble each other considerably, and there is no doubt that

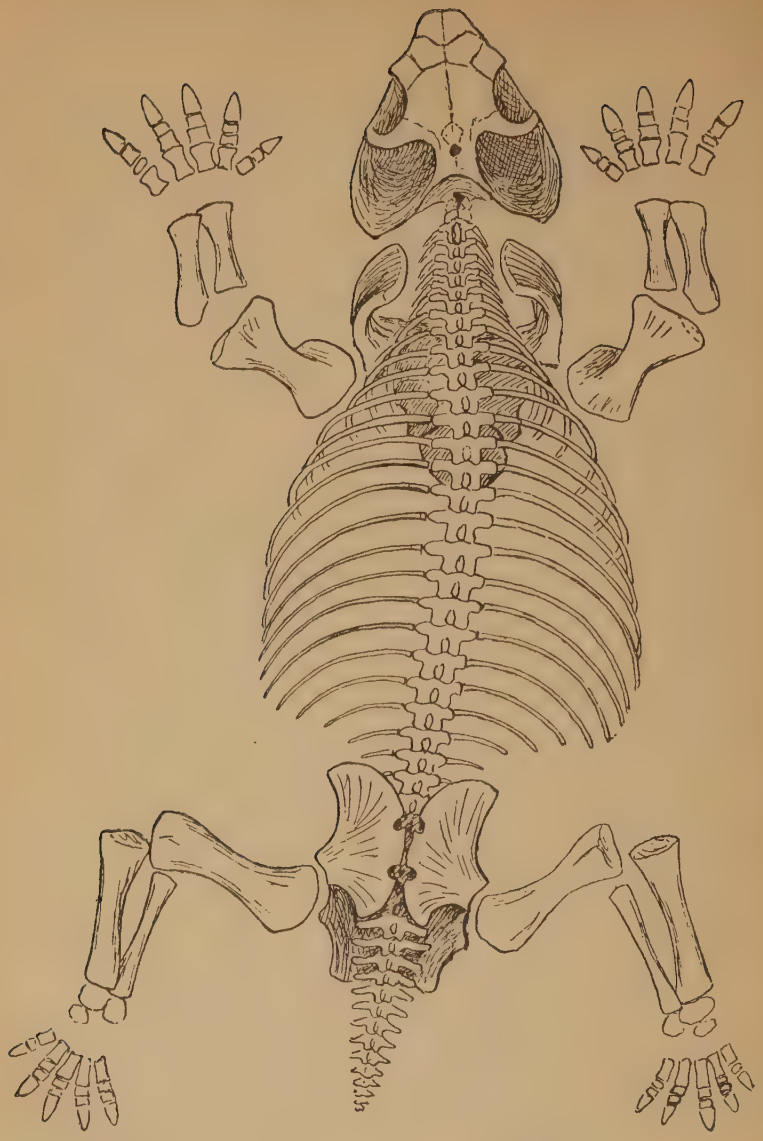


FIG. 4.—Skeleton of *Lystrosaurus declivis*, Owen—a semiaquatic Anomodont. About one-sixth natural size.

through one of these groups passed the line that gave rise to the mammals. In each group the teeth are specialised into incisors, canines and post-canines. The limbs are moderately long and slender, and there is little doubt that in general appearance they were more like mammals than typical reptiles, though doubtless the skin was scaly.

When we come to Triassic times we find a new type of carnivorous mammal-like reptiles, the Cynodontia. Though in outward appearance they resembled mammals probably less than the Gorgonopsians or Therocephalians, they approach the mammals more closely in many points of structure, as we shall see later.

The teeth are more like those of mammals, and there is a mammal-like secondary palate. For many years it was supposed that a Cynodont was the immediate mammalian ancestor, but we now know of a still more mammal-like group in the Rhœtic beds above the Triassic. This is the Ictidosauria.

These Ictidosaurians are small types which in almost all points of structure might be regarded as mammals except that the jaws still have the reptilian hinge. There can be no reasonable doubt, however, that all the mammals have originated from Ictidosaurian ancestors. It is, however, at present impossible to say whether the mammals have come from one Ictidosaurian or from two or three. The

FIG. 5.—Skeleton of the primitive Cynodont *Thrinaxodon liorhinus*, Seeley. About half-size.

earliest adequately known mammal, *Tritylodon*, is found in the same beds as the Ictidosaurians, and it is possible that the multituberculate mammals arose independently of the other groups. As they died out in Eocene times, and are not ancestral to any living forms, we need not give them any further consideration.

The monotremes, or egg-laying mammals, of Australia are the most primitive of living mammals, and some zoologists have been so impressed by the many points in which they differ from all the rest of the mammals that they have suggested their having had a quite different origin. The present writer, however, considers that the points of resemblance are much more striking than the differences, and believes that they separated off from the main mammalian line in Mesozoic times rather than independently from an Ictidosaurian reptile. The marked similarity of the ear ossicles in the two groups can hardly be explained in any other way than that the common ancestor was already a distinct mammal. The living monotremes are very valuable in giving us some hint of the structure of the Mesozoic mammals.

Although our knowledge of the mammalian ancestors in Permian and Triassic times is good, unfortunately we know comparatively little of the evolution of the mammals during the Jurassic and

Cretaceous times. We know a considerable number of jaws, a few skulls and one or two limb-bones. Fortunately this gap in our knowledge is not so serious as would at first sight appear. Already in the Rhœtic we have true mammals, and we are probably very safe in assuming that the earlier Jurassic carnivorous mammals were small forms allied to the monotremes, but without the specialisations of the head seen in the living egg-laying types.

When we come to Cretaceous times we find that already there are typical marsupials and insectivores, but the palæontological evidence is too scanty to tell us clearly how they arose, and we have to rely on our study of living forms and their development for an understanding of the steps in the evolution.

The marsupials are clearly related to the monotremes, and, as we shall see later, the very young marsupial still has a shoulder girdle that is practically monotreme; and the step from the marsupial to the higher mammals is a small one. But here again palæontology helps us little.

From the Basal Eocene to recent times we have very full evidence of the steps in the evolution of a large number of the modern types of mammals, artiodactyls, perissodactyls, elephants, carnivores and apes. But quite a number of orders appear to have originated before the Eocene, and of these we

know very little. In the Eocene we find well-developed lemurs, but have no palæontological evidence of their origin in Cretaceous times. From what we know of living forms we can, however, fill in the gap with considerable probability.

Of living mammals those which come nearest to the lemurs below them are the tree-shrews and elephant-shrews, the flying lemurs (*Galeopithecus*) and the bats. And of these the latter three are considerably specialised, so that the tree-shrews, the Tupaiids, appear to be the nearest relatives of the lemurs below them; and we are probably safe in assuming that the lemurs arose from a form allied to *Tupaia*, or at any rate from one of the order to which it belongs, the Menotyphla.

Then again there are a number of very interesting marsupial characters found in the Menotyphla, some of which are not likely to have been developed twice independently, and we are forced to assume that they indicate an affinity. We are thus led to the conclusion that probably in early Cretaceous times a primitive marsupial, of which perhaps the bandicoot (*Perameles*) is the nearest living representative, gave rise to a primitive member of the Menotyphla, and that one of the Menotyphla gave rise in Upper Cretaceous or Basal Eocene times to a primitive lemur.

The further evolution towards man is fairly

clear. The early lemurs gave rise to primitive Tarsioids, of which the living *Tarsius* is a much-specialised descendant.

The true apes appear in Oligocene times, and are pretty manifestly descended from Tarsioids. Whether the South American Platyrhine apes have come from primitive Old World apes, or vice versa, or whether the Old World and New World apes have been independently developed from Tarsioids, cannot at present be determined with certainty. Possibly the Old World apes and the New World apes are independent branches from a Tarsioid ancestor.

In Miocene beds of India and Europe we find numerous species of an anthropoid ape, *Dryopithecus*. Unfortunately little is known besides the lower jaw; but the evidence is quite satisfactory that in the Miocene there were anthropoids allied to the chimpanzee already in existence.

The step from the anthropoids to man is bridged by at least three intermediate stages.

Australopithecus, the very young child-ape found fossil at Taungs in South Africa, is the most important of the links. It is an anthropoid ape about the size of the chimpanzee, but differing in quite a large number of characters, and in all the characters in which it differs it approaches man. The most striking of the human characters is the condition

of the milk molars. In the chimpanzee and gorilla the milk molars are very different in pattern from those of man. In *Australopithecus*, though the teeth approach in size those of the gorilla, the patterns are almost exactly similar to those of man. There can thus be little doubt that *Australopithecus*, though an anthropoid near in general structure to the chimpanzee, is on or near the line that resulted in man, and thus closely allied to the ancestral anthropoid, if not the actual ancestor.

All the living anthropoids are forest or woodland forms. *Australopithecus* was in habits like the baboon, living partly on the plains and partly among the rocky krantzes.

The next step towards man is a big one. *Pithecanthropus*, the ape-man of Java, is known by the greater part of the brain-case, a couple of teeth and a thigh-bone. By the discoverer, Dubois, the thigh-bone is believed to belong to the same individual as the brain-case, and nearly every anatomist has accepted this view. As, however, there has been discovered in the same deposit a fragment of jaw which seems to be of a much higher human type than the brain-case of *Pithecanthropus* it seems probable that we are dealing with two humanoid species, and the thigh-bone seems more likely to have belonged to the second.

If we take the brain-case and molars as all we

know of *Pithecanthropus*, then it is manifest we have a being intermediate between the anthropoids and man, but much nearer to man than to the anthropoids. The brain-case is estimated to have had a capacity of about 850 cc., as against a human capacity averaging from 1200 c.c. to 1500 c.c. *Australopithecus* probably when adult had a capacity of from 500 c.c. to 600 c.c.

The third step towards man is represented by the Piltdown man, *Eoanthropus*, which has a large human brain but still an ape-like jaw.

The discoveries that are being made in China of the primitive man *Sinanthropus* are likely to add much further detail to our knowledge, but are unlikely to alter our present views.

There are many varieties of primitive man, Neanderthal man, Rhodesian man and Heidelberg man, but these are probably all side branches from the main line, and not ancestral, though possibly they may have interbred with the human types which led to *Homo sapiens*.

CHAPTER II

THE EVOLUTION OF THE SKULL IN FISHES, AMPHIBIANS AND PRIMITIVE REPTILES

As of course cartilage is very rarely preserved as a fossil, palæontology throws very little light on the earliest developments of the skull, and we can only conjecture what happened from what we see in the earliest developmental stages of the sharks.

Possibly the first parts of the skull to develop were cartilages to support the upper and lower jaws, and also cartilages to support the gill arches. But as soon as the anterior part of the neural canal became specialised as a brain some sort of skeletal support became necessary, and as the base of the brain was probably the most liable to injury, from the movements of the jaws and their muscles, probably the first structures to develop would be a pair of cartilaginous bars in front of the notochord, lying on the two sides of the pituitary. These are the bars found in all craniate vertebrates, and which are called the trabeculæ.

Other structures were soon developed. Cartilaginous capsules developed to protect the olfactory and auditory organs, and lateral cartilaginous bars

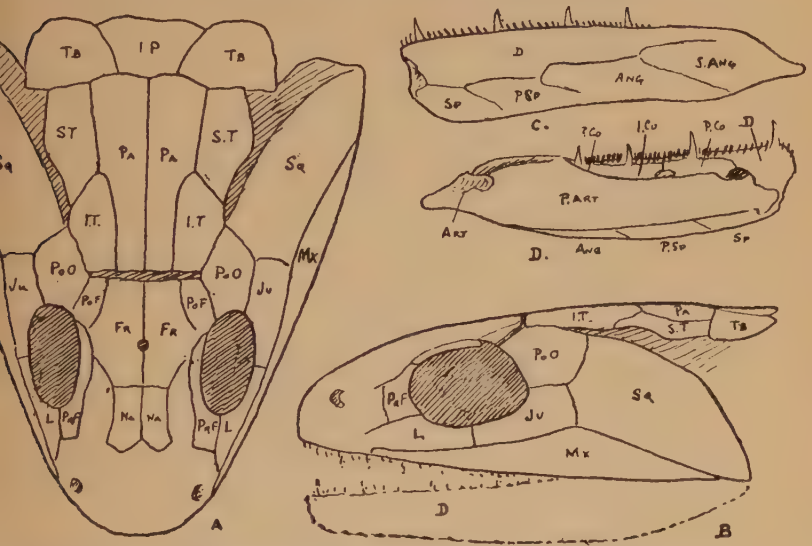
connected these pairs of capsules, and formed further protections for the brain. And basal cartilages developed by the sides of the front of the notochord, between the auditory capsules.

These developments constitute practically the whole of the primitive cartilaginous skull; and, though many changes take place by the addition of bones, the cartilaginous foundation remains essentially the same right up to man.

As already stated, the early Devonian fishes we know are mostly fresh-water or estuarine forms, and practically all, even those belonging to quite different groups, have developed bony scales; and the bony scales not only cover the body, but the skull and the jaws. The body scales are relatively small, to allow of movement of the body, but those on the head, where there is little movement, are usually much larger, and form a complete armour. We know no fish that we can say is certainly the first ancestor that had bony plates on the head, but *Osteolepis* gives us at least a fair hint of what the skull of the bony-scaled fish may have been like.

Quite a number of restorations of the skull of *Osteolepis* have been published. Unfortunately they differ considerably, but that published by Watson in 1926 is probably as accurate as can be at present given. On the top of the skull there are three pairs

of bones, and these pretty safely may be identified with the bones which we call in the higher vertebrates nasals, frontals and parietals. We can even feel quite sure that the nasals, frontals and parietals



G. 6.—*A*. Skull of lobe-finned fish of the Devonian *Osteolepis macrolepidotus*. Mainly after Watson. *B*. Side view of lobe-finned fish of the Devonian *Osteolepis macrolepidotus*. Mainly after Watson. *C*. Outer view of left mandible of the lobe-finned fish *Megalichthys*. After Watson. *D*. Inner view of left mandible of the lobe-finned fish *Megalichthys*. After Watson. Much reduced.

found in man are directly descended from these three pairs of bony plates or scales in this primitive rhipidistian fish. Round the eye there are six bones, and five of these can be traced up to the amphibians and reptiles—viz. the lacrimal, the jugal, the postorbital, the postfrontal and the prefrontal; and

two of them up to the mammals and man—viz. the lacrimal and the jugal, or malar.

Five other bones we can with confidence follow into the amphibian skull—viz. the supratemporal, the intertemporal, the squamosal, the tabular and the interparietal; and, of these, two can be traced up to man—namely, the squamosal and the interparietal.

The side view of the skull of *Osteolepis* shows the maxilla and the premaxilla. This latter, however, is not clearly distinct from some other elements in the snout.

The palate is not well known in *Osteolepis*, but is fairly well known in the allied *Eusthenopteron* of America. Here it will be seen that the roof of the mouth is bordered by the premaxillaries and the maxillaries, all bearing small teeth, and a pair of bones which may be the quadratojugals. Inside the premaxillaries are on each side three bones, which are manifestly the prevomers, the palatines and transpalatines of amphibians and reptiles. Of these bones only the premaxillaries, the maxillaries and the palatines can be traced up to man. Inside the palatines and transpalatines are a pair of large pterygoids. These are manifestly the same bones as can be traced right through the amphibians and reptiles to the mammals and man.

The mandible is not very well known in either

Osteolepis or *Eusthenopteron*, but is fairly well known in the allied *Rhizodopsis*. It agrees rather closely with the primitive amphibian jaw, a large number of bony plates surrounding the cartilaginous jaw—or Meckel's cartilage, as it is called in the higher vertebrates — and four of the elements support teeth.

The bony plates on the top of the skull have been spoken of as modified bony scales, but this is manifestly not a satisfactory explanation of the bones of the palate and those of the inside of the jaw.

In the fishes above the sharks the bony scales appear to have originated from a large number of small denticles becoming united by a bony plate developing at their bases in the skin; and this tendency to have teeth united on a bony framework is even more manifest in the mouth, and it is this that accounts for the large number of bones in the mouth of the Rhipidistians.

The teeth on the edges of the upper jaw give rise to the development of the premaxillaries and the maxillaries. On the roof of the mouth there are a large number of other teeth, some much larger than any borne by the premaxillaries and maxillaries. And these teeth on the palate give rise to the prevomers, the palatines, the transpalatines and the pterygoids. They also give rise to a large medium bone on the fish's palate—the so-called

"parasphenoid," a bone which I hope to show is the mammalian vomer.

In the lower jaw there is a row of teeth on the outer edge. This has resulted in the development of the main tooth-bearing bone of the jaw—the dentary. Inside the outer row is a broad row of small teeth, and these have resulted in the development of three coronoid bones, the coronoid, the intercoronoid and the precoronoid; and these correspond roughly with the transpalatine, the palatine and the prevomer of the upper jaw. Still further in, and down, is another row of teeth, and in connection with it is developed the principal bone of the inside of the jaw—the prearticular, or goniale. This might be considered as corresponding to the pterygoid of the upper jaw.

On the outside of the jaw are four scale-like bony plates, which also form the lower border of the jaw, and these same bones, as the evolution advances, pass round to the inside of the jaw. These are the splenial, the postsplenial, the angular and the surangular.

Of these nine new bones developed in the fish's jaw all are found in the early amphibians, and six of them in most reptiles. In mammals, where the jaw is greatly simplified, only the dentary is well developed, but the angular becomes the mammalian tympanic, and the prearticular is also present as a

small ossification near the upper end of the tympanic, and occasionally a small ossification is present which represents the surangular.

In the Rhipidistia, such as *Osteolepis*, in addition to the large number of bones of the skull just mentioned, which may be looked upon as surface bones, there are quite a number of internal bones. These latter are formed by ossification of the cranial cartilages. Practically the whole of the cranial cartilages became ossified, but we do not at present know how many bones this represents, as too few specimens are known, but probably as many as nine bones are developed.

It will be seen that we have thus two kinds of bones occurring in a skull—those which are formed by the ossification of cartilages and those which have no cartilage, but develop in membrane; and it is thus customary to distinguish bones into what are called cartilage bones and membrane bones. The names are convenient but not very appropriate, as the bones after development are exactly similar in structure, and there is no cartilage in a cartilage bone and no membrane in a membrane bone.

The cartilage bones that are most probably present in the lobe-finned fishes are the basioccipital, the exoccipitals, the opisthotics, the prootics, the quadrates, the basisphenoid and the presphenoid.

And in the lower jaw there is the articular as an ossification of Meckel's cartilage.

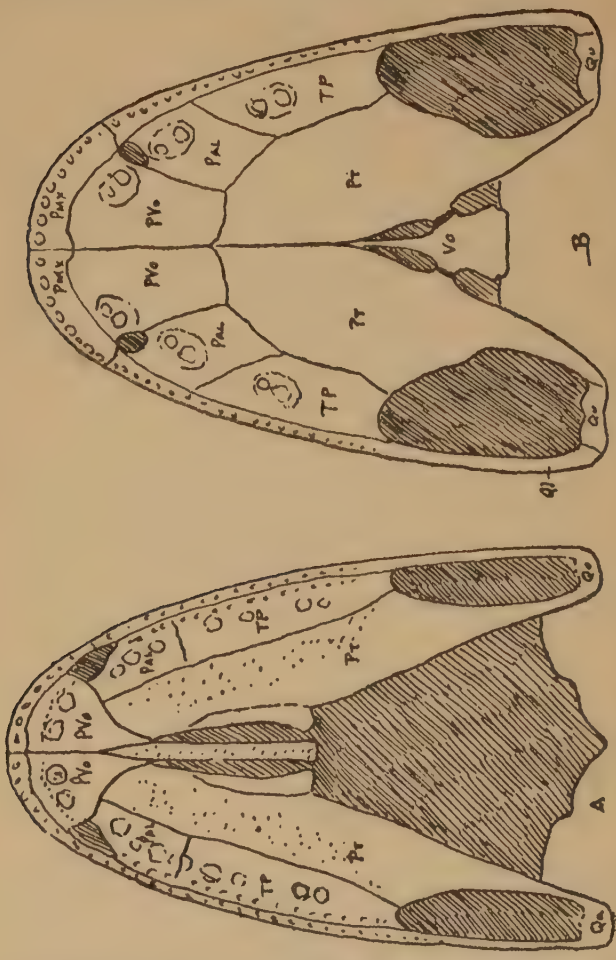


FIG. 7.—*A*. Palate of the lobe-finned fish *Eusthenopteron*. Partly after Bryant. *B*. Palate of the primitive amphibian *Baphetes*. After Watson.

Very little is known of the hyoid and branchial apparatus in these higher fishes.

In tracing the evolution of the skull and other parts of the skeleton from the fishes to man it is unnecessary to consider the side lines; and thus nothing need be said on the structure of the skull in the bony fishes of to-day or on the interesting, but highly specialised, skulls of the lung-fishes.

Though the step from the lobe-finned fishes to the tetrapod amphibian is a considerable one, and one that involved many changes in the internal organs, the changes in the skull are less than one would readily have anticipated.

Watson has revealed to the world the structure of the carboniferous amphibians, and these are doubly interesting, not only by being nearer to the fishes than the better-known later forms, but also because it is moderately certain that the line to the reptiles and mammals led through them, while it most probably did not pass through any of the higher labyrinthodonts.

The outer bones of the skull are well seen in *Palæogyrinus*. The top view of the skull is seen to agree fairly closely with that of the lobe-finned fish *Osteolepis*, except that in the fish there are opercular and apparently spiracular openings no longer present in the amphibian, or at least no longer affecting the skull; while the skull of the amphibian is now one firm structure instead of there being

some degree of movement in the middle of the skull of *Osteolepis*.

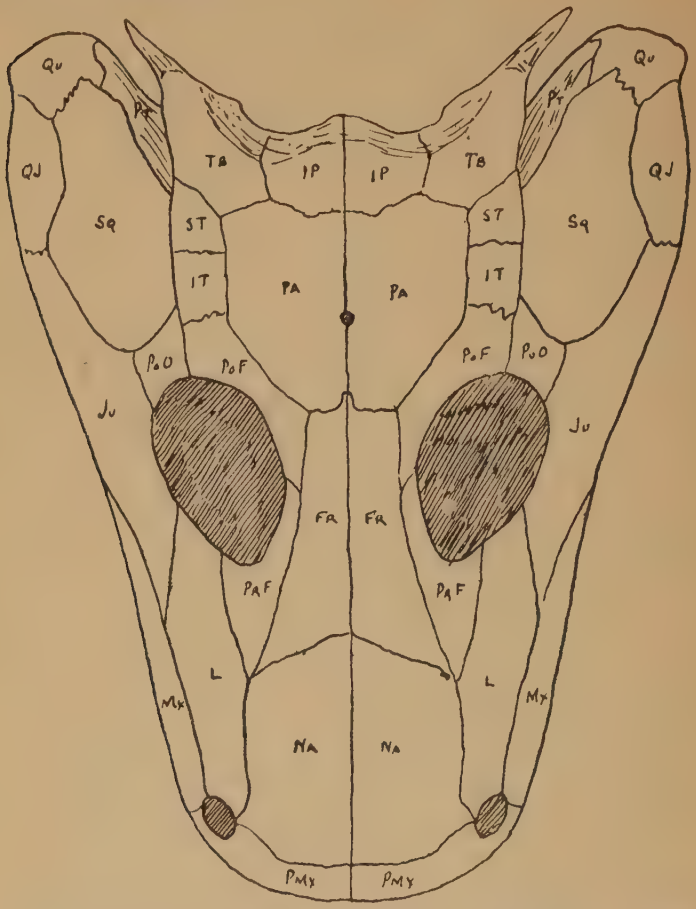


FIG. 8.—Skull of primitive Carboniferous amphibian *Palæogyrinus decorus*. Two-thirds natural size. After Watson.

Palæogyrinus has a skull which is sufficiently primitive and generalised to have been near the

type from which all later tetrapod skulls have been derived. In the middle line we have four pairs of bones—the nasals, the frontals, the parietals and the interparietals. These four elements we have already seen in the fish, though there the interparietal is unpaired. This interparietal bone, present from the fishes up to the mammals, has caused a good deal of confusion in nomenclature, and even in most of our text-books to-day is wrongly named. Formerly the posterior pair of bones in the labyrinthodont skull were believed to be supraoccipitals. Then when it became apparent that they are membrane bones they were called dermosupraoccipitals or dermoccipitals. But, as I pointed out some years ago, they are certainly the bones that have for many years been called interparietals in mammals, and must therefore be called interparietals in these lower forms in which they occur.

Round the eye are five bones—the jugal, the lacrimal, the prefrontal, the postfrontal and the postorbital. All five can be traced up to the reptiles. In the temporal region are five bones—the quadratojugal, the squamosal, the tabular, the supratemporal and the intertemporal. Of these, the first two are found in most reptiles; the third in many, and one of the others in a few; but whether this one is the supratemporal or the intertemporal

is uncertain, and thus the nomenclature is here in doubt.

Round the jaw are two premaxillaries and two maxillaries.

The palate is not fully known in *Palæogyrinus*, but is satisfactorily known in the allied *Baphetes*. From the figure given, it will be seen that the tooth-bearing bones agree closely with those in the lobe-finned fishes, though the base of the skull is evidently much smaller. Inside the premaxillaries and the maxillaries are the prevomers, the palatines and the transpalatines, with inside these others, large pterygoids. There can be seen a part of the basioccipital which forms the hinge of the skull. In front of this is a triangular bone which supports the pterygoids. This is the bone which in most text-books is called the "parasphenoid," but which is really homologous with the mammalian vomer and ought to be called the vomer. At the back of the temporal openings are seen the quadrates, on which the lower jaws hinge.

The skulls of most of the later amphibians agree in many ways with the skulls of *Palæogyrinus* and *Baphetes*, but differ in having a large opening between the anterior median process of the vomer and the pterygoids. As these later amphibians are not on the mammalian line of descent we need not further consider them, but reference may be made

to the best known of modern amphibians, the frog, in order that certain erroneous determinations of the bones may be corrected.

In all text-books the median bone seen on the under side of the skull is called the parasphenoid.

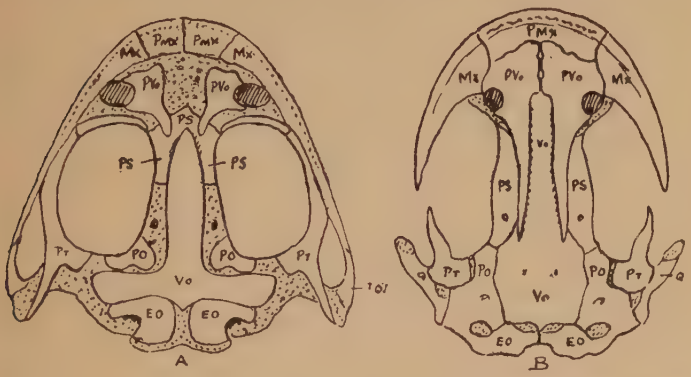


FIG. 9.—Palatal view of the skull of (*A*) an Anuran amphibian *Rana*; and (*B*) a Urodele *Molge*. Both enlarged.

This is the bone seen in *Baphetes*, and which will be shown to be the mammalian vomer. In front of the brain-case is a large median cartilage bone. In most text-books this is called the sphenethmoid; in some it is called the *os en ceinture*, or girdle bone; in some the ethmoid. Even the name alisphenoid has been applied to it. It will presently be shown that it is the mammalian presphenoid. In the front of the palate are two bones called in all text-books the vomers. These will be shown to be prevomers.

As already mentioned, we do not know exactly

from which amphibian or group of amphibians the first reptiles have been derived. If the Permian form *Conodectes* (*Seymouria*) is really a reptile, then almost certainly the reptiles arose from an amphibian such as *Palæogyrinus*. But, for reasons which it would be out of place here to state at length, *Conodectes* is regarded by the writer as an amphibian, which has come to have a few reptile-like characters, but which is not on the reptilian line. And, though one may be quite unable at present to say what amphibian was ancestral to the reptiles, attention may be called to the fact that there are large numbers of small forms too imperfectly known to enable us to say anything of their skull structure, or even to classify. One remarkable tiny skull from the Permian of America, *Gymnarthrus*, may be the only known representative of a group of amphibians which may have been ancestral to the reptiles. In any case the structure is suggestive.

Gymnarthrus is a tiny little amphibian with a skull only about three-quarters of an inch long, and unfortunately nothing is known of it except the skull. The top shows four pairs of bones in the middle line, the nasals, the frontals, the parietals and the interparietals. In front of the small orbit are the prefrontals and the lacrimals. In the temporal region are a long postfrontal, a postorbita

nearly as long, a large squamosal and a small tabular and quadratojugal. The side view shows the shallow maxillary and the long jugal. The quadrate is apparently partly exposed.

The palate is remarkable for the large size of

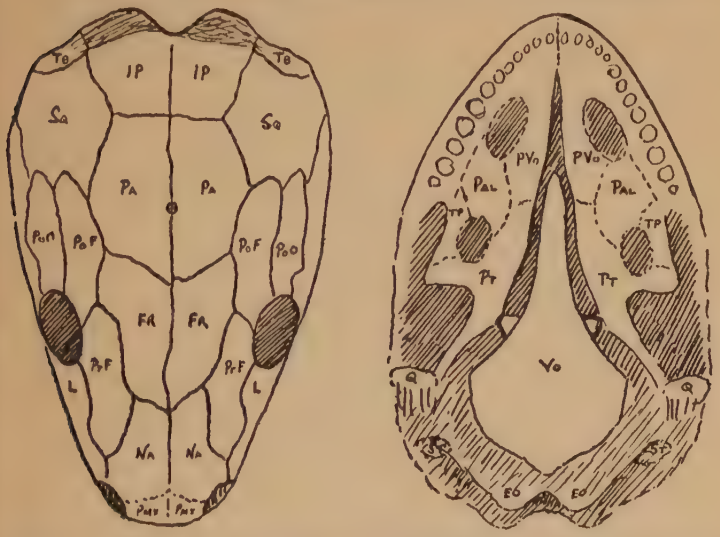


FIG. 10.—Upper and lower views of skull of the Lower Permian amphibian *Gymnarthrus*. About four times natural size.

the vomer (parasphenoid). By the sides of it are apparently two small bones for articulating with the pterygoids. These may be the basiptrygoid processes of the basisphenoid, or more probably they are independent elements which are known in lizards and in *Conodectes*, and whose origin is not yet quite clear. The palatines, prevomers, transpalatines and pterygoids are all rather slender, and

recall in a number of ways the corresponding bones in *Lysorophus*, which is believed to be a primitive urodele, and which is certainly an amphibian. The skull has two large occipital condyles as in most amphibians.

The lower jaw is like that of amphibians in retaining a large postsplenial; though it is well to remember that a postsplenial is also found in the primitive reptile *Pantylus*.

If the discovery of the postcranial skeleton of *Gymnarthrus* proves it to be an amphibian, then the case for its being an amphibian near the origin of the reptiles will be strong, as it certainly foreshadows in many ways the early reptiles, of which *Captorhinus* and *Labidosaurus* may be taken as types.

The earliest true reptile's skull adequately known is that of *Captorhinus augusticeps*, and a figure is given of the palate of this species. For the upper and side view of the skull I give figures from another hitherto undescribed species, *Captorhinus gregoryi* (Am. Mus. 4760).

The top view of this skull shows the same elements as are seen in the *Gymnarthrus*, but with the proportions very different. There is a very large pineal foramen, and the frontals and parietals are large. The interparietals and tabulars are, on the other hand, relatively small.

The side view shows the maxillary as a slender

bone and the lacrimal as relatively very large, and stretching from the orbit to the nostril. The squamosal is seen to be very large and the quadratojugal small.

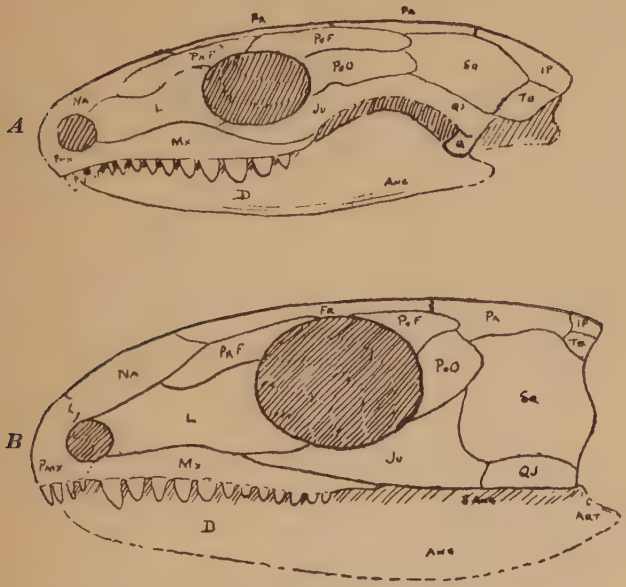


FIG. 11.—*A*. Side view of the Lower Permian amphibian *Gymnarthrus*. Enlarged. *B*. Side view of skull of the Lower Permian primitive Anapsid reptile *Captorhinus gregoryi*. (Am. Mus. 4760.)

The palate is very interesting, and is of the generalised type from which all reptilian palates seem to have been derived. The prevomers are small, and lie between the internal nares, and posteriorly, as in the living *Sphenodon*, meet the pterygoids. The palatines are relatively large and

the transpalatines rather small. Each pterygoid is very long, and as in typical reptiles has a long anterior branch to meet the prevomers, a long posterior branch to articulate with the quadrate,

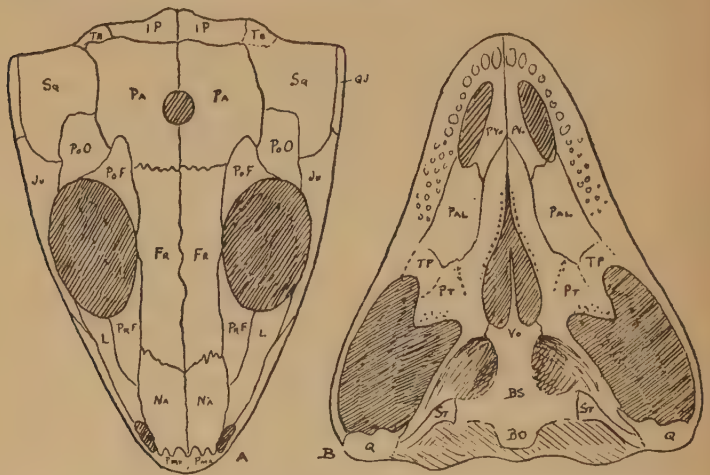


FIG. 12.—*A*. Upper surface of skull of Anapsid reptile *Captorhinus gregoryi*. *B*. Palatal surface of skull of Anapsid reptile *Captorhinus augusticeps*.

and a short transverse portion approaches the inner side of the mandible. Between the pterygoids there is a moderate-sized median space, in which lies the narrow anterior process of the vomer (the "parasphenoid" of most authors). It is unknown how far back the vomer passes, as the sutures in the posterior part of the base of the skull cannot be made out. The vomer, or possibly the basisphenoid covered by the vomer, gives an articulation to the

pterygoids. On each side, between what must be the otic bones and the quadrates, are seen the stapes. This stapes, or columella auris, is apparently homologous with the hyomandibula of the fishes. Being a loose bone it is usually lost in fossil skulls.

There is a single occipital condyle.

From a skull somewhat similar to that of *Captorhinus* the skull of all later reptiles can be easily derived. *Captorhinus*, as we have seen, has the temporal region completely roofed, and all primitive reptiles agree in this respect, and are placed in a super-order, Anapsida. Many Permian forms are known with this roofed temporal region, and a few still survive into the Triassic; but with the increase in development of the temporal muscle, openings were formed in the roof to allow more room for the contracted muscle, and all modern classifications of the reptiles are founded on the way these openings have occurred.

In one large group of reptiles the opening has taken place at the point where the squamosal, the postorbital and the parietal meet. The reptilian orders in which this type of opening is met with are the Mesosauria, the Ichthyosauria, the Plesiosauria and the Placodontia. And in the opinion of the writer the Chelonia are a further modification of the same type, by the loss of the bar behind the opening.

In Upper Permian times a second opening took place in addition to the first, and a new group originated, from which most later reptiles have sprung. These reptiles with two temporal openings form the super-order Diapsida, and include the Phytosauria, the Crocodilia, the Eosuchia, the Gnathodontia, the Rhynchocephalia, the Saurischian and Ornithischian Dinosaurs and the Pterosauria. The Squamata are descended from Eosuchia, with the loss of the jugal-quadratojugal bar; and the birds have come from a Diaptosaurian ancestor allied to the ancestors of the Pterosauria.

But the student of mammalian descent is only indirectly concerned with those reptiles which have a supratemporal opening, or two temporal openings, since the mammals have come by another line.

It seems probable that the supratemporal opening arose in narrow-headed types, and that the two openings are due to forms which had already the supratemporal opening becoming secondarily broad-headed. Forms which continued broad-headed, like the ancestral *Captorhinus*, developed only a lower temporal opening at the point of union of the squamosal, the postorbital and the jugal. Such reptiles form the large and important super-order Synapsida, and as it is from one of these that the mammals certainly arose we must confine our attention mainly to this super-order.

In the Permian of both America and South Africa we find very primitive members of the Synapsida. In America a number of orders and sub-orders are known, but the classification is

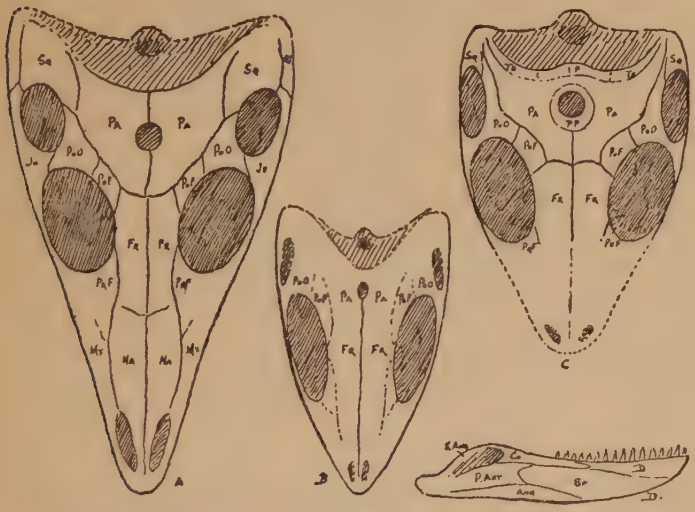


FIG. 13.—*A*. Upper view of skull of primitive Theromorph reptile *Eumatthevia bolli*, Broom. Natural size. *B*. Upper view of skull of primitive Theromorph reptile *Glaucosaurus megalops*, Williston. *C*. Upper view of Anningiamorph reptile *Anningia megalops*, Broom. *D*. Inner view of left mandible of *Glaucosaurus megalops*, Williston. All two-thirds natural size.

not at present quite satisfactory. The more primitive forms are probably nearly related to the ancestors of those mammal-like reptiles we find a little later in South Africa, and it is these alone that we need consider. The later developments in America led to the fantastically spined pelycosaurs.

Of the primitive American types the best known are *Mycterosaurus*, *Glaucosaurus* and *Eumatthevia*. In South Africa we find *Anningia*, which may not be very closely allied to the American forms, but which nevertheless has a skull essentially similar in type.

Eumatthevia is known only by an imperfect skull and some post-cranial bones, but the main points of the cranial structure can be made out with certainty. The eyes are large, and in the lower temporal region on each side is a relatively small temporal opening. This opening is bounded by the squamosal, the jugal and the postorbital. The parietals are large, and the squamosals moderately large. The side view of the skull shows the relatively large quadratojugal situated exactly as in *Captorhinus*. In fact, but for the opening, the whole temporal region is almost exactly as in that more primitive form. The structure of the preorbital region cannot be determined with equal certainty. One would have expected in this primitive synapsid to find the lacrimal extended from the orbit to the nostril, as it does in the higher theromorphs—as these American synapsids are called—*Varanosaurus* and *Naosaurus*; but the evidence so far as it goes is in favour of the lacrimal being quite short, and in the allied *Mycterosaurus* it is also short.

The palate is not sufficiently preserved to enable

one to give a satisfactory figure, though most of the elements can be easily identified. It is essentially similar to the palate of the higher theromorphs such as *Dimetrodon*.

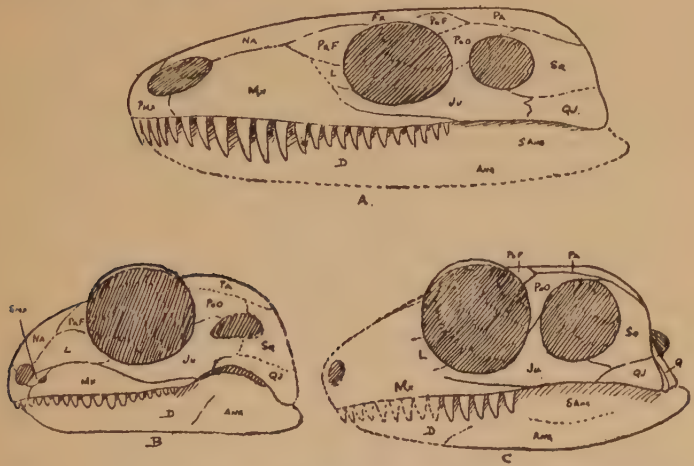


FIG. 14.—*A*. Side view of skull of the primitive Theromorph *Eumatthevia bolli*, Broom. *B*. Side view of skull of the primitive Theromorph *Glaucosaurus megalops*, Williston. *C*. Side view of the Anningiamorph reptile *Anningia megalops*, Broom. All two-thirds natural size.

Glaucosaurus is known by only one rather badly preserved skull. It is remarkable for having quite a short snout and a very small temporal opening. Here the lacrimal extends from the orbit to the nostril, and below it in front is apparently a small septomaxillary very similar in structure to what we shall presently see in the typical therapsids.

In the South African primitive synapsid *Anningia* there are a number of striking resemblances to the American types, and a few differences. The skull resembles that of *Glaucosaurus* in having very large orbits, and in having a short snout, but differs in having a very much larger temporal opening, though the opening is bounded by the same bones as in the American form. The top of the skull is strikingly similar to that of *Eumatthevia*, except that in *Anningia* there is a preparietal bone surrounding the pineal foramen and the interparietals and tabulars appear partly on the surface, whereas in *Eumatthevia* they are apparently entirely on the occiput.

In all the above three synapsids the mandible is essentially similar to that in *Captorhinus*. Both the angular and surangular are large, and form most of the posterior half of the outer side of the jaw. On the inner side is a large splenial, and well-developed coronoid and prearticular bones.

CHAPTER III

THE STRUCTURE OF THE SKULL IN THE THERAPSIDS, OR MAMMAL-LIKE REPTILES

In South Africa in Middle, or if we accept Schuchert's view in Upper, Permian times there arose a group of higher synapsids allied in many ways to the theromorphs of America, but differing in certain important characters and much more mammal-like, and which are placed in a super-order, Therapsida.

These therapsids form a group of reptiles nearly as varied as the living mammals, and fortunately they are now so well known that almost all details of structure have been satisfactorily made out, and the affinities can be traced even more satisfactorily than in mammals. The Upper Permian and Triassic are the only periods in the geological history before the Tertiary that are adequately known, and the great variety of forms seen suggest how very meagre is the record in other ages.

There are large therapsids belonging to the order Dinocephalia, with their sub-orders Titanosuchia and Tapinocephalia, some of which were probably sixteen to eighteen feet in length, and others thick-

set animals as large as a hippopotamus. Another order has small rat-like forms with long, running legs. Still another group has forms with broad, fantastically shaped skulls. But these we need not consider, as they are somewhat off the mammalian line of descent.

There is one order, however, to which reference must be made, though it is not in the direct line—the Anomodontia. Of this group the best-known genus is *Dicynodon*. And though the skull is so little like that of a mammal on superficial examination that neither Owen nor Huxley suspected any mammalian affinities, the postcranial skeleton is so very mammal-like that Owen referred some bones which were not associated with a skull to a form allied to the egg-laying mammals of Australia, and even suspected they might belong to an ancestor, and yet the skull is essentially similar to that of the mammal, though greatly specialised.

The top view shows large temporal openings, but it is interesting to observe that the parietal bone is still shut off from the opening by the meeting of the postorbital and squamosal bones, and though the skull is very unlike that of, say, *Eumatthevia*, the temporal opening is formed by exactly the same bones—the postorbital, squamosal and jugal. The squamosal is of enormous size, and its anterior process extends even to below the orbit, and

articulates with the maxillary. In some species the septomaxillary is large, and forms a considerable

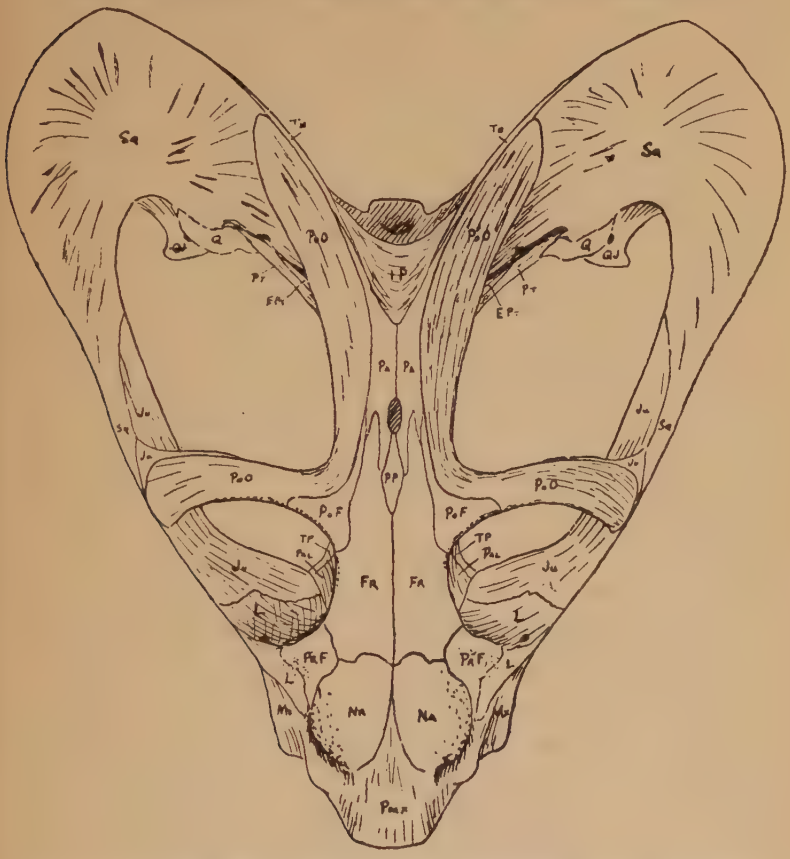


FIG. 15.—Upper view of skull of the Anomodont reptile *Dicynodon kolbei*, Broom. About half natural size.

part of the face; in others it is entirely within the nostril. The postfrontal is relatively small, and is largely hidden by the meeting of the frontal and

postorbital above it. The premaxillary is a large medium bone, always single, though of course it may have been developed from two centres of ossification. In some species the ascending process is so large that it almost completely divides the nasals.

The palate is very highly specialised, and very unlike that of either the typical reptile or mammal. Curiously enough, it bears considerable resemblance to that of the chelonian, though not at all nearly related. The interesting points to be noticed in the palate are the huge median premaxillary, the rudimentary secondary palate formed by the maxillaries and palatines, the absence of a transverse process in the pterygoid, the short thick stapes, and the large quadrate and quadratojugal fused together. In the structures round the internal nares *Dicynodon* is approaching the mammals: in the structure of the quadratojugal and quadrate it is primitive. In all other points it is highly specialised and aberrant.

The median section of the skull is extremely interesting. The base of the skull is seen to have three bones, in the middle line of which the posterior two are manifestly the basioccipital and the basisphenoid. The anterior bone has long been known, but until recently its exact determination has been in doubt. It has usually been called the ethmoid or sphenethmoid, and it pretty certainly was homologous with the sphenethmoid of the frog. As will

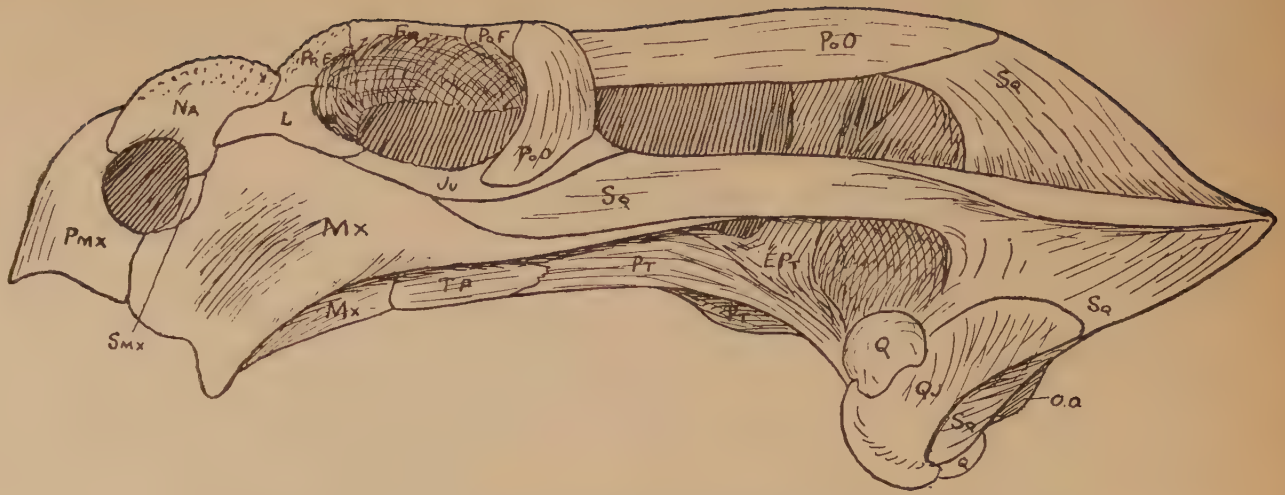


FIG. 16.—Side view of skull of the Anomodont reptile *Dicynodon kolbei*, Broom. About two-thirds natural size.

be shown presently, it is certainly the homologue of the mammalian presphenoid.

In front of the basisphenoid is a long slender process with a groove along its upper side. This manifestly is the homologue of the bone that in typical reptiles and amphibians has been called the parasphenoid. It will be seen to occupy a position very similar to the vomer in mammals, and certainly like the vomer forms a floor to the median cartilage. It differs only in being early ankylosed to the basisphenoid. As will be shown presently, the vomer in *Ornithorhynchus* entirely agrees with this bone in *Dicynodon* in being very early ankylosed to the basisphenoid. We can thus conclude that it is the true vomer. The large prevomer is seen below the vomer.

In the Upper Permian there are two main suborders of carnivorous therapsids—the Gorgonopsia and the Therocephalia. They are closely allied, and both very mammal-like, and it has been a matter of considerable difficulty to determine through which of them the mammalian line lay. The Gorgonopsia appear to have the stronger claim.

The top view of the gorgonopsian skull shows a most interesting and primitive arrangement of the bones. The temporal region is broad, and the temporal opening, though large, is formed by the same bones as in the early types—the squamosal,

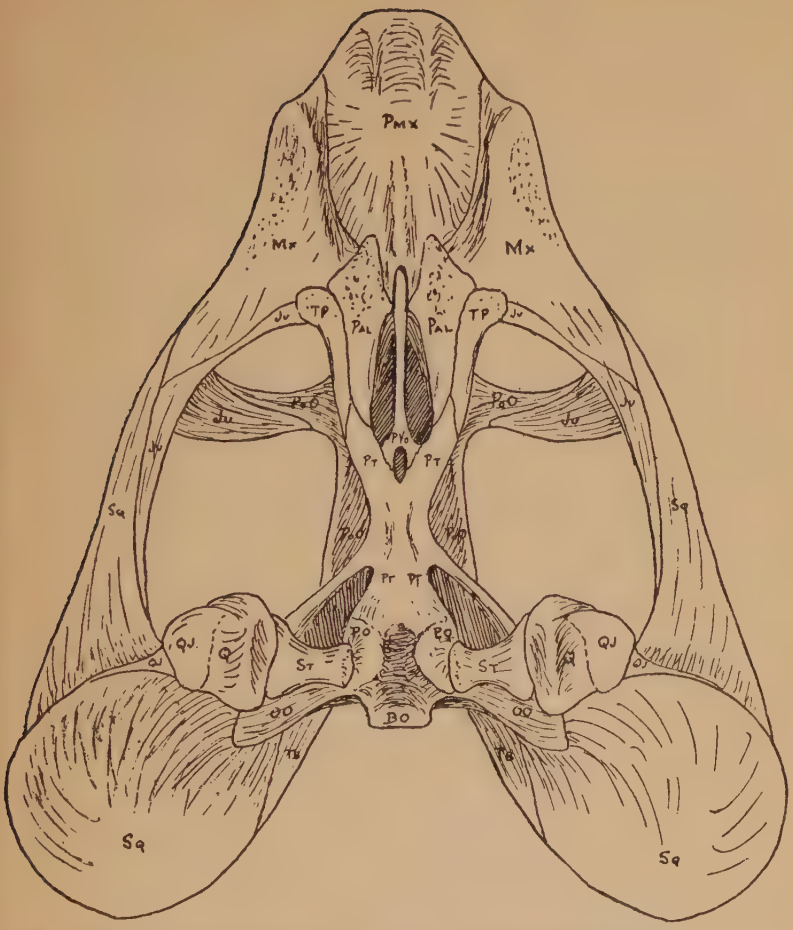


FIG. 17.—Palatal view of skull of *Dicynodon kolbei*, Broom
About half natural size.

the jugal and the postorbital. The postfrontal is large, and there is generally a large preparietal bone as in anomodonts and *Anningia*. Whether this preparietal is a new bone or a dermal bone that has been inherited from the fishes is uncertain. In many of the early fishes we find a median bone that might easily correspond. Even in some amphibians, such as *Eryops*, there is a large median bone situated between the anterior ends of the frontals. Possibly the preparietal is this same bone which has shifted back. More probably it is a median bone which has been situated between the parietals and frontals and retained. It is not found in any forms after Triassic times. Most of the other bones of the top and side of the skull are very like those of mammals.

The palate is very interesting. There is no secondary palate, but on the sides of the palatines there are indications that a soft palate carried the internal nares well back. In the front of the palate is a long median bone. This is the fused prevomers. Posteriorly it meets the pterygoids, but the palatines meeting in the middle line below them hide the point of union. Between the long posterior processes of the pterygoid there is a large median bone. This was formerly believed to be the basisphenoid, but is now known to be the vomer. It is certainly a membrane bone, which extends forward between the pterygoids and even overlaps the basioccipital

behind. The basisphenoid is completely hidden by it. The quadrate is of moderate size, and a small quadratojugal is attached to its outer side. The

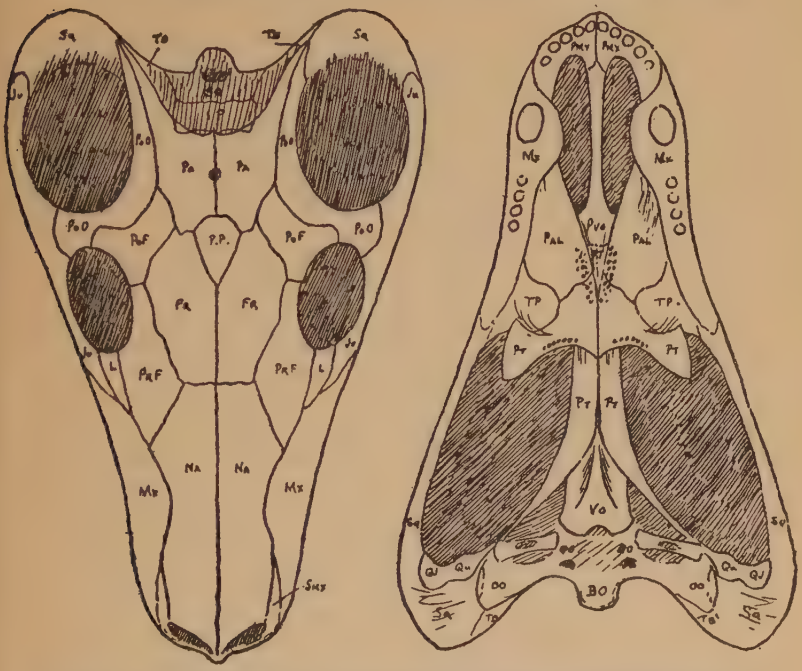


FIG. 18.—Upper and lower views of skull of the Gorgonopsian reptile *Scylacops capensis*, Broom. About two-thirds natural size.

stapes is a short rounded bone with a large foramen. The occipital condyle is single.

There are usually five incisors, which certainly replace an earlier set; but whether there are more than two sets is unknown. The canine is large, and there seem to be no fewer than four canines

succeeding one another. There are usually from two to six simple little molars, and no clear evidence has been brought forward of replacement, though possibly it occurs.

The lower jaw is essentially similar in gorgonopsians and therocephalians. On the outer side are seen a large dentary, which forms about two-thirds of the jaw, and has a well-developed coronoid process, a small surangular and articular, and a large angular which has a peculiar outer plate. In the cavity between the outer and inner plates of the angular was probably lodged the submaxillary gland.

On the inner side of the jaw are seen a large splenial, a small thin coronoid bone and a long slender prearticular.

In the Therocephalia the skull differs in a number of points. The temporal fossæ are very large, and a median parietal crest is formed and the squamosal secondarily pushed back from the postorbital. The parietal region is thus much more like that of the mammal. In other respects the top and side of the skull are very similar to those of the gorgonopsians.

The palate differs from that of the Gorgonopsia in there being a large opening between the pterygoid, the palatine and the transpalatine.

In other points the palate is very similar to that

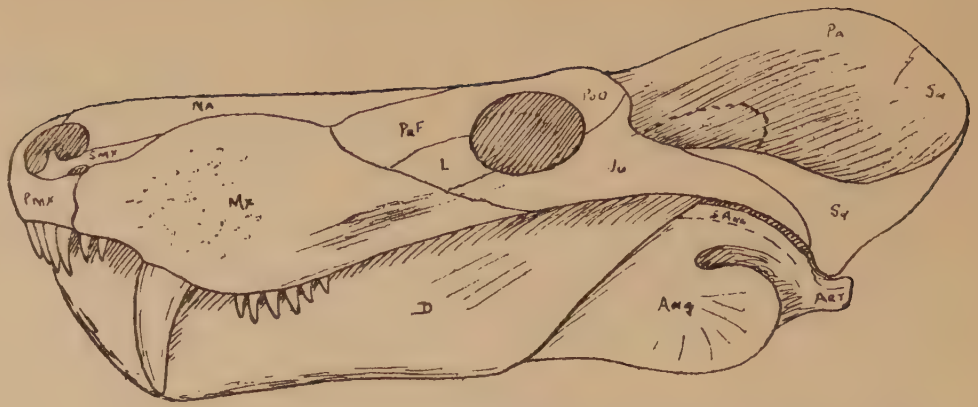


FIG. 19.—Side view of skull of a Therocephalian (*Pristerognathus vanderbyli*, Broom). About one-third natural size.

of the gorgonopsians. The vomer in some forms however is very small.

The Cynodontia, which is the principal group of carnivorous therapsids found in the Trias, show many points of advance towards the mammals from the sub-orders of the Permian. It is generally agreed that the mammalian line came through the Cynodontia, though the higher types of cynodonts are much too specialised to have been the mammalian ancestors.

The top and side views of the skull of the earlier cynodonts are strikingly like those of mammals. The important differences are that the brain in the cynodonts is very small and there is a pineal foramen. Also, in the cynodonts there are prefrontal and postorbital bones. As in the therocephalians, the temporal fossa is large and the postorbital no longer meets the squamosal above the fossa. There is a well-developed septomaxillary.

The palate differs considerably from that in the Permian therapsids, but especially in there being a well-developed secondary palate which is strikingly like that of mammals. In the lower cynodonts, such as *Platycraniellus*, we see how the palate is formed. Here it is still incomplete, so far as the bones are concerned, by the plates of the maxillaries and palatines only approaching in the middle line. In

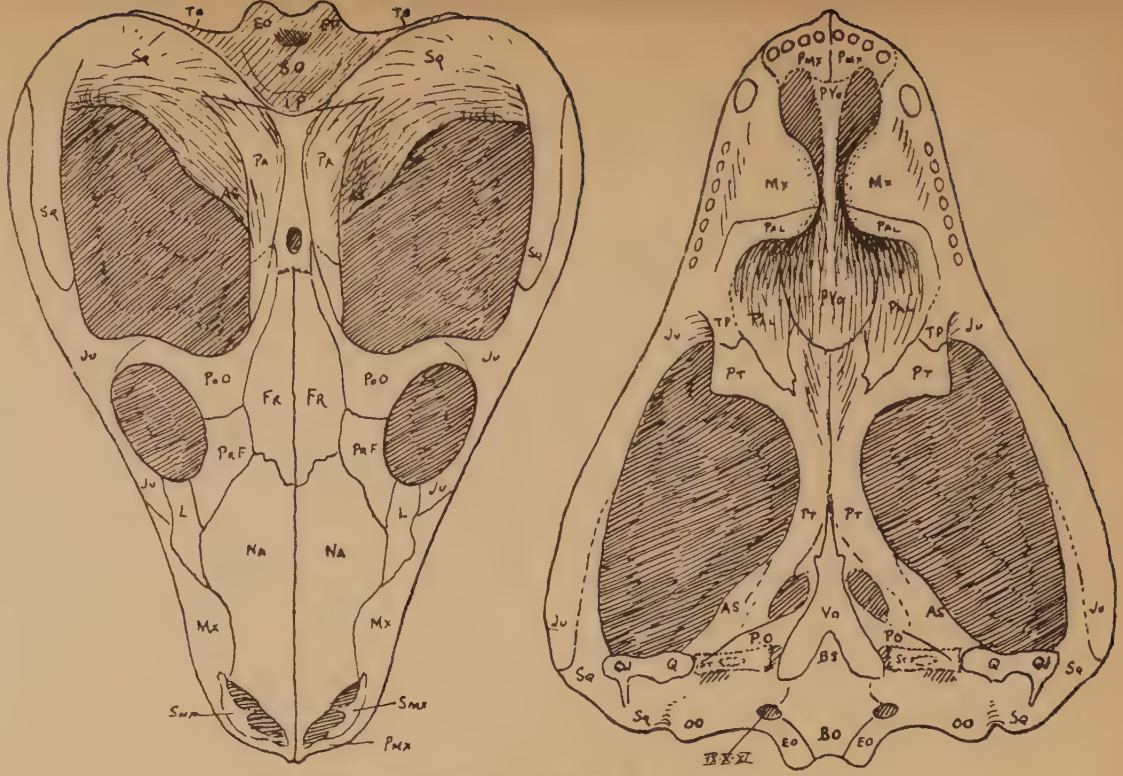


FIG. 20.—Upper and lower views of the skull of the primitive Cynodont reptile *Glochinodontoides gracilis*, Haughton. Natural size.

the large majority of cynodonts the secondary palate is complete.

A secondary palate carrying the internal nares far back is a character by no means confined to mammals and their ancestors. To have the nares carried back so that respiration need not be interfered with by eating was such an advantage that nature brought about the development in a large number of different groups. Of living animals, the crocodiles have an even better developed secondary palate than the mammals, and most birds, and many lizards, have at least an imperfect secondary palate developed, and among the therapsids it seems probable that a secondary palate has been developed independently in at least four different groups. A small therocephalian is known with an imperfect palate not unlike that of *Platycraniellus*. In another sub-order, the Bauriamorphs, there is a complete secondary palate, and in the anomodonts there is a rudimentary secondary palate.

But though the secondary palate of the cynodonts is very similar to that of the mammals there is one striking difference. In the mammal the palate is supported by the median true vomer; in the cynodont the median supporting bone is the prevomer, or rather the fused prevomers, and the true vomer is quite small and far back, and under the base of the brain. This difference is so great that for a

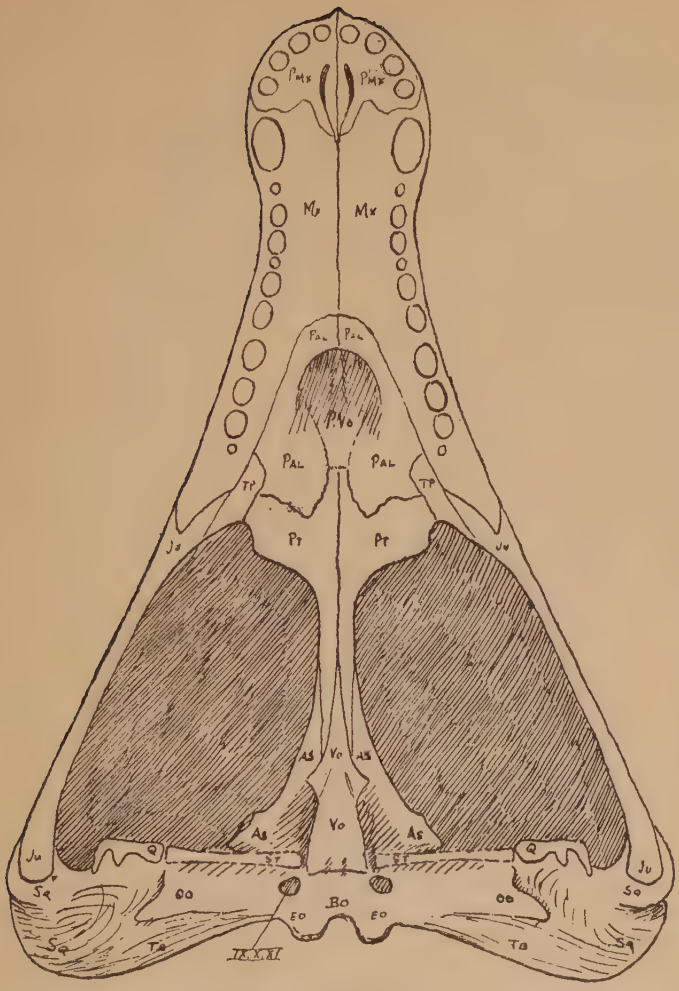


FIG. 21.—Palatal view of skull of the higher Cynodont *Cynidiognathus longiceps*, Haughton. About two-fifths natural size.

time it seemed to rule out the cynodont from the mammalian ancestry. But the discovery of a higher group, the Ictidosaurians, has given us the clue. As the brain increased in size in small cynodonts the vomer was carried forward and the prevomer became reduced.

The quadrate and quadratojugal are similar to those of the therocephalians and gorgonopsians, but much smaller.

Another interesting change seen in the cynodont skull is that the epipterygoid, present as a slender rod in most primitive reptiles, and still as a narrow, rounded pillar in the gorgonopsians, and a flattened prop in the therocephalians, becomes in the cynodont a fan-shaped flat bone which at once becomes manifestly the homologue of the mammalian alisphenoid.

The occipital condyle, which in the earlier therapsids is rounded and typically reptilian in structure, becomes in the cynodonts, by the reduction of the basioccipital, a double condyle, formed mainly by the exoccipitals.

The lower jaw is characterised by the dentary forming in the early cynodonts about three-quarters of the jaw, and in the later cynodonts almost the whole jaw when viewed from the outside. Inside are seen all the other jaw elements found in the lower therapsids, but they are relatively

small, and though the articulation is formed by the articular on the quadrate, the dentary in the higher types almost reaches the squamosal.

In beds which are considerably later geologically than those in which the cynodonts occur, and which

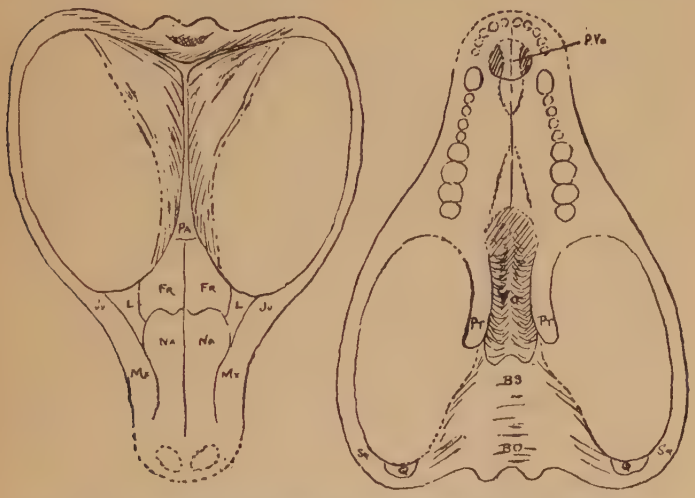


FIG. 22.—Upper and lower views of skull of Ictidosaurian reptile. About one-and-a-quarter times natural size.

are either Rhœtic or Lower Jurassic, a new group of therapsids is formed which practically forms the connecting line between the cynodonts and the mammals. Of this sub-order, which is called the Ictidosauria, the best-known example is a small animal about the size of a rat, which has not yet been named. The skull differs from that of all the earlier therapsids in having lost the prefrontal and

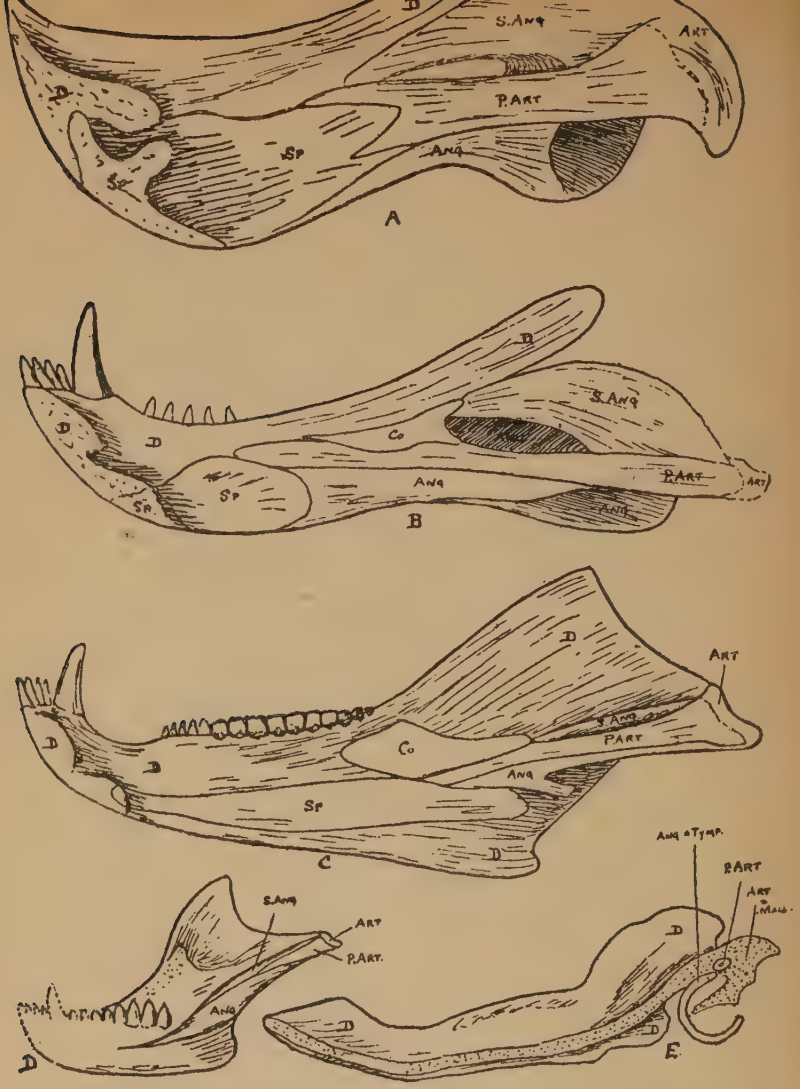


FIG. 23.—The inner sides of mandibles of various Therapsids and a mammalian embryo.

A. Inner side of the right mandible of the Anomodont *Lystrosaurus*. *B*. Inner side of the right mandible of a young Gorgonopsian *Cynarioides*. Enlarged. *C*. Inner side of the right mandible of the Cynodont *Gomphognathus*. Reduced. *D*. Inner side of the right mandible of an Ictidosaurian. *E*. Inner side of the right mandible of an embryo rabbit. Enlarged. (After Gaupp.)

In the toothless and somewhat degenerate Anomodont mandible the coronoid is lost, and there is only a rudimentary coronoid process. In the Gorgonopsian we have a good example of the primitive Therapsid condition. In the Cynodont the chief advance is seen in the great development posteriorly of the dentary. In the Ictidosaurian the dentary is still greatly developed. The coronoid and splenial are lost and the other elements much reduced. In the mammal the articular, prearticular and angular are specialised and retained as auditory ossicles.

postorbital bones, and in having no trace of a postorbital arch. There is also no trace of a pineal foramen. In fact, except that the brain is relatively small, the skull when viewed from above is much more mammalian than therapsid. The palate, though not fully known, can be restored with confidence. The most interesting point is that, with the relatively great increase of the brain and the shortening of the snout, the vomer, which in the cynodont is far back, is here advanced almost into the mammalian position. It passes far forward, and I think it likely that it supports the secondary palate as in mammals. And most probably the prevomer is greatly reduced, as in *Ornithorhynchus*. There are two large occipital condyles, as in mammals.

The lower jaw is almost entirely formed by the dentary, as in mammals, the other bones being much reduced. The splenial has apparently disappeared, and also the coronoid bone. A small articular hinges on a small quadrate, and the articular is supported by a small prearticular, a small surangular and a larger angular, which is lodged in a groove on the inside of the dentary. Had the mode of hinging of the jaw not been discovered this small fossil animal would by most have been regarded as a mammal.

CHAPTER IV

THE STRUCTURE OF THE MAMMALIAN SKULL

THE most primitive mammals available for the study of the evolution of the skull are the monotremes, or egg-laying mammals of Australia — *Ornithorhynchus* and *Echidna*. There are of course quite a considerable number of mammals known from Triassic, Jurassic and Cretaceous rocks, but unfortunately few are known by anything but jaws, and though the Eocene Multituberculate *Ptilodus* is known by much of the skull, and the Rhœtic *Tritylodon* by a good snout, we have hardly sufficient facts to enable us with confidence to settle their affinities, and in any case they are not in the direct line to the higher mammals.

The monotremes are also off the main line, but we know their skulls fully and they throw much light on the early mammalian conditions. Unfortunately both the living monotremes are greatly specialised; and though on superficial examination they appear so different that one might fancy he had two very distinct types to study, the two are really so closely allied that we have only slight variations of one type.

The skulls of *Ornithorhynchus* and *Echidna* are figured in many of our text-books, usually rather badly. In both monotremes the sutures close early, and unless one has young specimens the limits of the bones are difficult to determine.

The skull of the young *Ornithorhynchus* shows many unusual characters, and at first sight looks very unlike that of the therapsids. The parietals are very large, and the frontals small. There is no interparietal but a very large supraoccipital. The snout by being converted into a beak presents a most unusual development. The whole snout is broad and much flattened. The premaxillaries are pushed apart, and above them lie a pair of septomaxillaries. The nasals are very large and the maxillaries long and well developed. The jugal is quite small and lies above the long zygomatic process of the maxillary. On the side of the brain-case are two bones that have caused some trouble. Behind the orbital plate of the frontal is a bone which forms a considerable part of the cranial wall. This is certainly orbitosphenoid, and behind this, and below the lower border of the parietal, is a large membrane bone whose affinities are in doubt. Watson calls it the anterior process of the periotic. It occupies the position of the alisphenoid in higher mammals, and the fact that it is a membrane bone does not prove that it is not an alisphenoid. In marsupials most

of the alisphenoid is formed in membrane, and I think this element, when its development is fully worked out, will prove to be the alisphenoid.

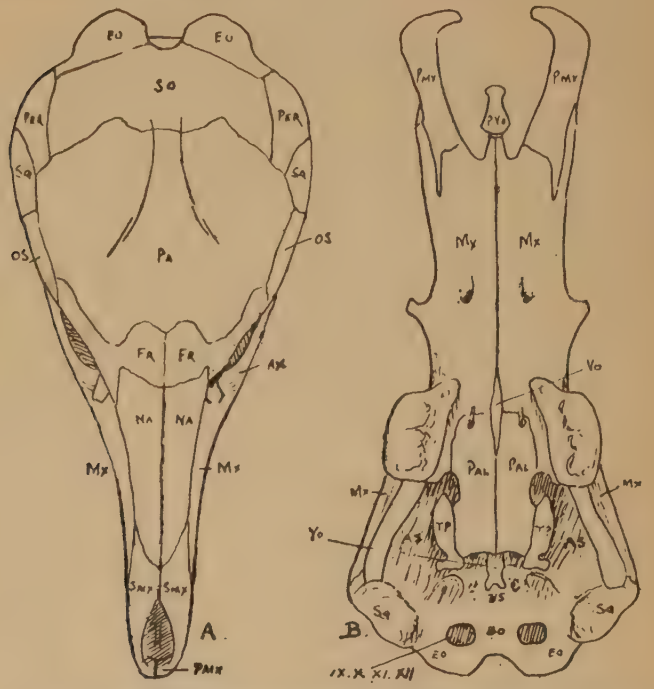


FIG. 24.—*A*. Upper view of skull of *Echidna lewisi*. Natural size. *B*. Palatal view of skull of *Ornithorhynchus anatinus*. Natural size.

It is here necessary to say something about the orbitosphenoid, a bone which we have not met with in the lower forms. In all the lower types of amphibians and reptiles we have found in the front cranial regions a median cartilage bone which

generally surrounds part of the brain. In all the lower forms, when this element is ossified it appears to ossify as a single bone, which I have argued is homologous with the mammalian presphenoid. In mammals the side wings through which usually pass the optic nerves have independent centres of ossification, and are thus entitled to be regarded as distinct bones, and these have been called the orbitosphenoids. They occur in all mammals, and though in a sense they also occur in the reptiles, being there ossified as parts of the presphenoid, they are not regarded as distinct bones.

The base of the *Ornithorhynchus* skull is as interesting as the top and sides. There is a very long secondary palate formed by the maxillaries and palatines, with a large part of the vomer appearing in the middle between the palatines and maxillaries. In front of the maxillaries is a most interesting median bone. This was formerly called the dumbbell-shaped bone, and its affinities were in doubt. Newton Parker first showed that it is a paired bone, with the two sides uniting early.

A little later I showed that, as it supports the Organ of Jacobson in exactly the same way as the little paired "vomers" in the lizards do, this dumbbell-shaped bone must be really homologous with the so-called "vomers" of the lizard. And as *Ornithorhynchus* has a large true vomer, quite distinct

from the dumbbell-shaped bone, a new name was required for the anterior pair of vomerine bones, and I proposed the name "prevomers." And it is undoubted that the paired bones in the bird, the lizard and the amphibian are prevomers.

There is another bone in the monotreme skull that has given rise to much difficulty. In both *Ornithorhynchus* and *Echidna* there is seen outside the posterior part of the palatine a bone which at first sight might be regarded as pterygoid, and which in fact has nearly always been called pterygoid. It is large in *Echidna*, and comparatively small in *Ornithorhynchus*. When, however, sections are made of a young skull, or a young skull carefully dissected, there is found to be another bone lying by the side of the nasal passage inside the palatine. And there seems no doubt it is this small bone that is the pterygoid. What then is the outer bone? Gaupp, who first showed that there are two pterygoid bones, called the large outer one the "Echidna-pterygoid," for convenience. It is unnecessary here to discuss the question at length. It seems to me that the bone is a transpalatine, which, with the great extension backwards of the secondary palate, has been carried far back, and has come to some extent to replace the true pterygoid.

The auditory ossicles are essentially similar to those of the typical mammals, though the incus is

very small and the stapes columelliform. The tympanic membrane of the ear is supported by the tympanic bone.

The change from the reptile to the mammal is, so far as the skeleton is concerned, essentially a change in the articulation of the jaw. So long as the jaw hinged on the quadrate the jaw had to remain a snapping jaw, but with the development of soft movable cheeks and compound molar teeth freer movement became possible and advantageous, and the dentary which in many cynodonts and Ictidosaurians nearly reaches the squamosal began to take up a second articulation with it. As soon as this arose the other small bones of the jaw became free from the dentary, and kept up their attachment with the quadrate, and came to take a greater part in the auditory function. The quadrate became the incus, and the articular the malleus. Of the membrane bones two survive in all mammals: the angular, which becomes the tympanic bone, and the prearticular, which remains as a small ossification at the head of the tympanic. In some mammals a trace of the surangular also remains.

A median section of the skull of a young *Ornithorhynchus* shows some interesting characters. The base of the skull has three cartilage bones, of which the posterior two are the basioccipital and the basisphenoid. And well in front of the basisphenoid,

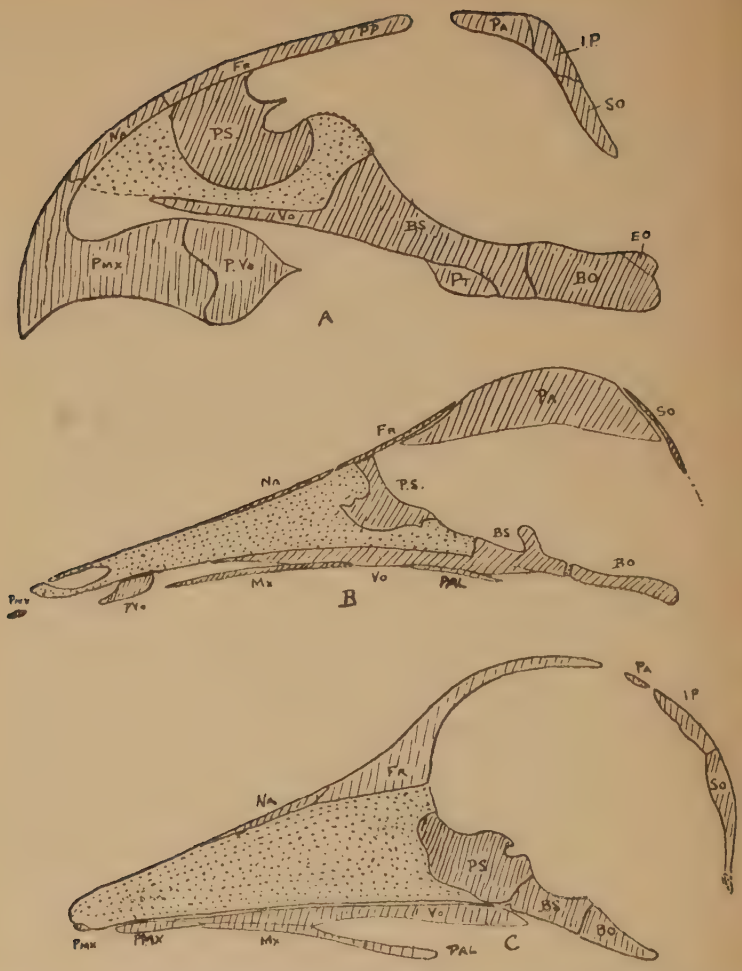


FIG. 25.—*A*. Median section of skull of *Dicynodon sollasi*. *B*. Median section of skull of young *Ornithorhynchus*. *C*. Median section of skull of young calf.

and practically occupying the position of the mesethmoid in the dog, is a third bone. As this bone, however, gives off from its two sides what are undoubtedly the orbitosphenoids it must necessarily be the presphenoid, and thus there is no trace of a mesethmoid. If the section be compared with that of *Dicynodon* the close agreement of these three bones will be manifest. Another interesting feature is the condition of the vomer. It is, as in the reptiles, very early ankylosed to the basisphenoid, and thus agrees in every respect with the so-called "parasphenoid." But as the vomer of *Ornithorhynchus* is undoubtedly homologous with the vomer in man the "parasphenoid" of the reptile must take the name vomer.

Most higher mammals which lack the specialisations seen in the monotremes are much more like the therapsids in the general appearance of the skull. In most books on osteology and natural history the skull of the rabbit or dog is taken as the mammalian type, and most of the bones are similar in the two, and typical of mammals generally.

Over the top of the skull in the dog are the usual bones seen in lower forms—nasals, frontals, parietals and interparietal. On the side of the skull are seen the premaxillary, the maxillary, lacrimal, jugal and squamosal. And on the side of the braincase are seen the orbitosphenoid, the alisphenoid

and the periotic. On the occiput we have the supra-occipital, the exoccipitals and the basioccipital.

On the base of the skull are seen, in addition to the premaxillary and maxillary, the palatines, the

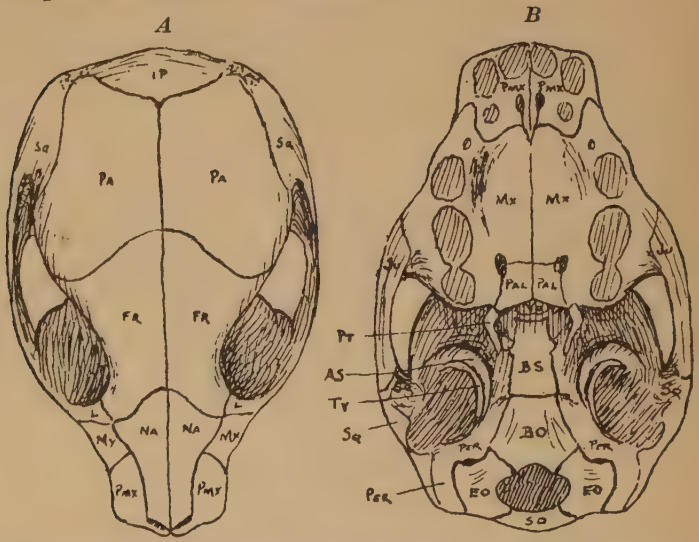


FIG. 26.—Skull of young Diprotodont marsupial *Trichosurus vulpecula*. Three times natural size. *A*. Upper view. *B*. Palatal view.

pterygoids and the vomer, and the tympanic forms much of the auditory canal.

On median sections there are seen to be four bones at the base of the brain. These are the basi-occipital, the basisphenoid, the presphenoid and a large bone called the mesethmoid. Until recently it was considered that as a mesethmoid is present in the dog and the rabbit it is typical of mammals

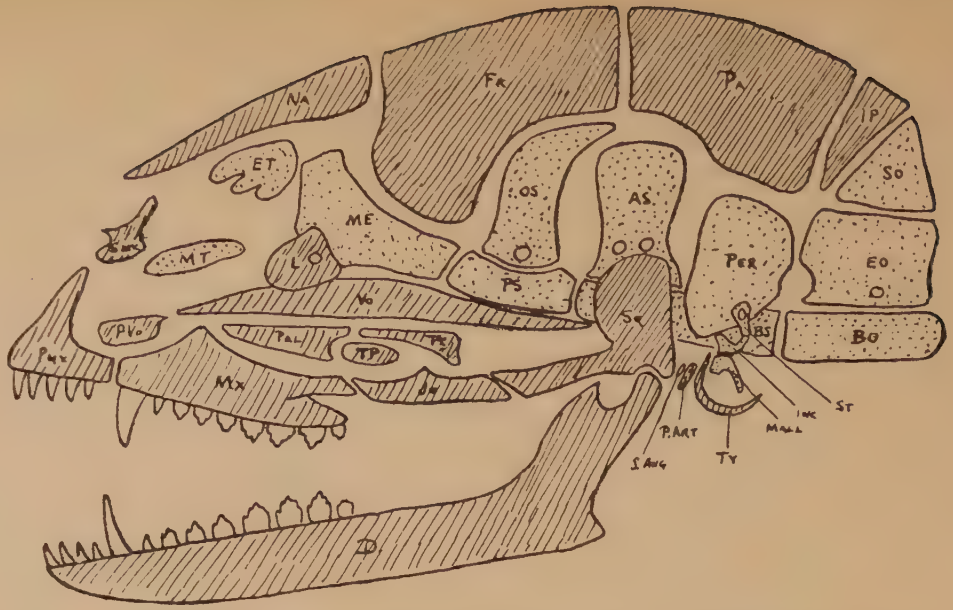


FIG. 27.—Diagram of the bones of the mammalian skull. Cartilage bones dotted, membrane bones shaded with lines.

and generally, or always, present. This, however, is by no means the case. Already it has been shown that there is no mesethmoid in the monotremes, and I have elsewhere shown that there is no trace of a mesethmoid in the marsupials, nor the armadillos, nor the sloth; nor in artiodactyls nor in perissodactyls, elephants, sirenians, nor in the little golden mole (*Chrysochloris*). A mesethmoid is present, however, in the pangolin, the hyrax, carnivores, rodents, insectivores, bats, lemurs, apes and man. In the Cetacea it is probable that one has been present and secondarily lost by degeneration.

It would seem that as the brain grew larger in the mammals too much of the median cartilage was left to be ossified by the presphenoid and a new ossification arose.

In the nose there are other ossifications. In the upper olfactory chambers, on each side, the cartilage foldings which support the chief part of the olfactory membrane ossify to form the ethmoturbinals. They unite early with the mesethmoid or presphenoid. In the lower part of the nasal cavity is usually an ossified maxilloturbinal. This supports the lower turbinal, and it is closely related to the lacrimal duct.

In all mammals the hyoid arch is more or less ossified, and generally there is an ossification representing the first branchial arch. But though we can

Fig. 28.—Median section of skull of young baboon (*Papio porcarius*). Natural size. Plates of the frontal meet in the middle line between the presphenoid and the mesethmoid, forming the interorbital septum.

examine the various modifications of the arches in living mammals, very little is known of the condition of the hyoid in extinct forms, as the apparatus is invariably loosely attached to the skull, and thus usually lost, while as the cartilaginous parts are

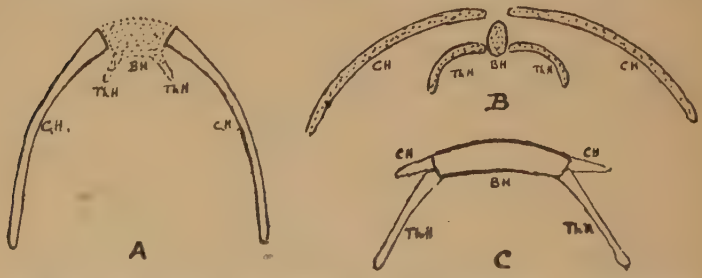


FIG. 29.—*A*. Hyoid apparatus in a Cynodont *Thrinaxodon liorhinus*. *B*. Hyoid apparatus in an embryo Diprotodont marsupial *Trichosurus vulpecula*. *C*. Hyoid apparatus in man.

not preserved as fossils it is difficult to identify the osseous elements even when present.

In fishes and urodeles a number of visceral arches are usually ossified. In *Lysorophus*, a Permian urodele, there are well-developed ossifications in no fewer than four arches.

In cynodonts there are a pair of long slender ossified elements which are probably the ceratohyals. All the other elements have apparently remained cartilaginous.

In living mammals the hyoid apparatus usually consists of a basihyal with, on each side, a ceratohyal in front and a thyrohyal behind. In ungulates

there are a series of elements on each side—usually a long stylohyal with a short epihyal and a short ceratohyal, and, behind, a small thyrohyal.

In man there is a large basihyal with a short ceratohyal and a relatively long thyrohyal.

The Human Skull.—The human skull differs but little in essentials from that of the typical higher mammals. It is merely a higher mammal skull in which the brain-case has become enormously developed and the rest of the skull correspondingly reduced.

The nasals, the frontals and parietals present no unusual characters, except in the great development of the latter two. The interparietal is early fused with the supraoccipital.

In the face there is one character that is unique among mammals. The premaxillary is so early co-ossified with the maxillary on the face that the two bones can hardly be recognised as distinct. On the palate, on the other hand, there is a well-marked suture between the premaxillary and the maxillary sufficient to show that the premaxillary is really present though there is no distinct suture between it and the maxillary on the face.

The jugal—or, as it is called in human anatomy, the zygomatic or malar—is similar in its relations to that of the higher apes. It differs from that in most mammals in having a large articulation with

the alisphenoid (the great wing of the sphenoid) at the back of the orbit.

The squamosal is present as the squamous portion of the temporal bone, and it agrees closely with

FIG. 30.—Median section of skull of newly born Kafir baby.

that of the mammals generally. The human temporal bone is composed of three elements—the periotic, the squamosal and the tympanic—and up to shortly before birth these three elements are quite distinct.

The human palate is very similar to that of typical mammals, and indeed differs little from that of the cynodonts. The secondary palate is formed as in these lower forms, by the premaxil-

laries, the maxillaries and the palatines. Behind the palatine is the pterygoid, which is present in the adult as the inner pterygoid process of the sphenoid bone. It is frequently called the hamulus pterygoideus.

The occiput is formed of five bones—the interparietal, the supraoccipital, two exoccipitals and the basioccipital. At birth only four are distinct, the interparietal being partly united to the supraoccipital; in fact, the interparietal is co-ossified with the supraoccipital in the middle region, though the sutures are distinct at the sides. The occipital condyles are mainly formed by the exoccipitals.

Articulating with the outer sides of the exoccipitals are the periotics or petrosals. These correspond to the fused prootics and opisthotics of the lower forms, but in man, as in most mammals, it is difficult to distinguish the two elements except at the commencement of ossification. Between the periotic and the exoccipital is the large foramen for the ix, x, and xi nerves. In the reptiles this foramen is between the opisthotic and the exoccipital, and it can be traced in the same position up to man.

At birth, lying underneath the middle part of the periotic, is seen the tympanic as a semicircular ring of bone. This supports the tympanic membrane of the ear, and in the adult the bone forms the

lower part of the bony tube which constitutes the external auditory canal.

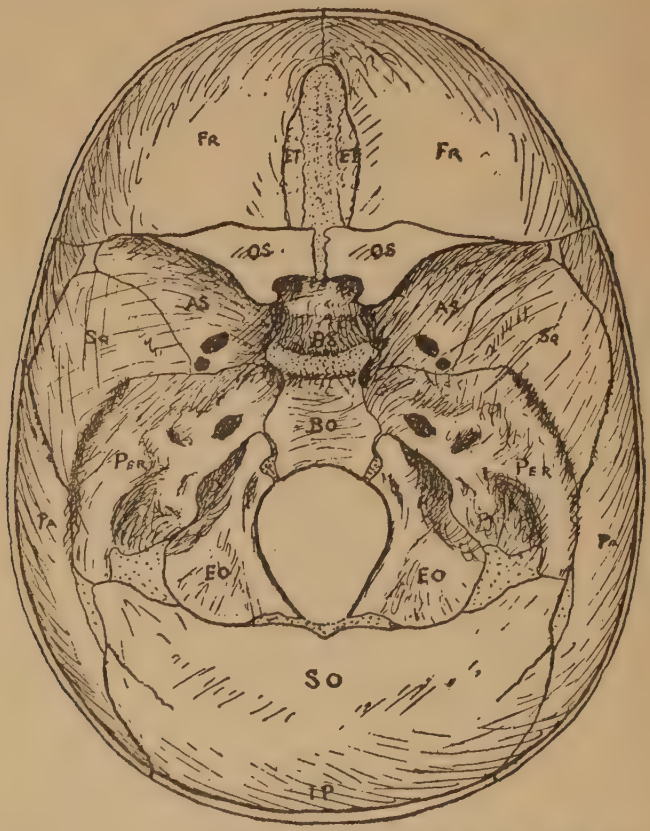


FIG. 31.—Inner view of the base of skull of newly born Kafir baby.

Within the tympanic, and in articulation with the lower part of the squamosal, can be seen the auditory ossicles—the malleus, the incus and the stapes.

In front of the basioccipital, the periotics and the squamosal lies a large complex bone, which in the adult is called the sphenoid bone or os sphenoidale. It is really a compound of the basisphenoid, the presphenoid, the two alisphenoids, and the two orbitosphenoids of the lower mammals, with, as has already been pointed out, the pterygoids. Even at birth these elements are already fused together, but at an earlier stage can be clearly seen as distinct elements.

The following is a list of the bones in the adult human skull, and the elements which are represented in them:

Occipital = basioccipital, exoccipitals, supraoccipital, interparietal.
Sphenoid = basisphenoid, alisphenoids, presphenoid, orbitosphenoids, pterygoids.
Ethmoid = mesethmoid, ethmoturbinals.
Temporal = squamosal, periotic, tympanic, stylohyal.
Parietal.
Frontal.
Nasal.
Lacrimal.
Maxilla = premaxilla, maxilla.
Inferior turbinal.
Palatine.
Jugal = malar, or zygomatic.

Malleus.
Incus.
Stapes.
Inferior maxilla or mandible.
Hyoid = basihyal, ceratohyal, first branchial.

CHAPTER V

VERTEBRÆ AND STERNUM

The Vertebræ.—In all vertebrate animals there have developed round the notochord a series of skeletal structures to give attachment to the body muscles, and to protect the spinal cord, which lies immediately above the notochord. In sharks, skates, and other primitive fishes, these skeletal structures consist of a series of cartilaginous plates, which are arranged in small groups by the passing out of the spinal nerves. These small groups of elements form the primitive vertebræ. It is unnecessary here to consider the details of the structure of these vertebral elements, as many different types are found in the early fishes, and it is not quite clear which elements go to form the elements of the vertebræ in the tetrapods. The difficulty is that the living sharks are not in the direct line of descent, while the ancestral lobe-finned fishes have had the vertebræ imperfectly ossified and the cartilaginous elements have not been preserved as fossils.

One of the best known of the early types of vertebræ is that of the fossil amphibian *Eryops*, and though *Eryops* is not an ancestor of the higher

vertebrates there is good reason to believe that the ancestor must have had vertebræ of the same type.

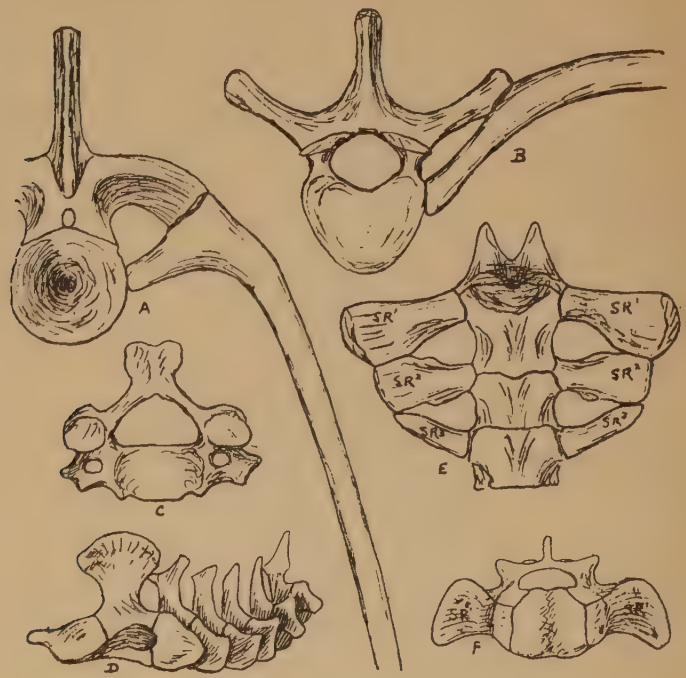


FIG. 32.—*A.* Dorsal vertebra with rib of Dinocephalian reptile *Moschops*. *B.* Dorsal vertebra with upper part of rib of man. *C.* Cervical vertebra of man. *D.* Axis and succeeding cervical vertebræ in nearly adult *Echidna*. *E.* Sacral vertebræ of Chelonian *Macrochelys*. After Williston. *F.* 1st sacral vertebra of young wombat.

This primitive type of vertebra consists of two upper elements which unite to form an arch over the spinal cord, two lateral elements which lie one on each side of the notochord, and two lower

elements which unite to form a basal portion. The arch has a large median process which passes upwards and is called the spine, and has two anterior and two posterior processes with articular surfaces for articulating with the adjacent vertebræ, and there is an outward process on each side, called the transverse process, which usually articulates with part of the rib. The lateral elements are relatively small, and articular with the bases of the arch. The lower element is larger, and normally gives an articulation to the head of the rib. The lateral portions are called the pleurocentra and the lower portion the hypocentrum.

In most lower, and in all higher, land vertebrates the vertebral elements encroach on the notochord, and may even completely obliterate it. The two pleurocentra enlarge, and then unite to form the centra of the vertebræ of higher forms, and the arches in the large majority fuse with the centra to form the vertebræ.

The hypocentrum in the reptiles becomes greatly reduced. It usually remains as the lower part of the first vertebra, or atlas, and in a large number of animals develops into the chevron bones found along the lower side of the tail vertebræ. In many reptiles the hypocentra remain as small ossifications between most of the centra, and these are called the intercentra. These small intercentra are

known to occur in some cynodonts, therocephalians and gorgonopsians, but apparently are absent in anomodonts. Except as the lower part of the atlas and as chevrons the hypocentra are absent in mammals.

Almost all the vertebræ have lateral outgrowths, which pass between the upper and lower groups of the body muscles in much the same way as the spines and the chevrons lie between the right and left muscle groups. These lateral developments are called costal elements, because they are specialised as ribs in the thoracic region.

The dorsal vertebræ of man are essentially similar to those not only of most other mammals but of most of the mammal-like reptiles. The centrum has completely obliterated the notochord, though traces of it can be detected even at birth. The centrum with small parts of each side of the arch form the body of each vertebra, and the anterior and posterior faces are practically flat. Between the flat ends of two adjacent vertebræ there is a thick intervertebral disc of fibrous connective tissue, which not only firmly connects the two vertebræ but acts as a pad to prevent jarring.[1] The arch of each vertebra has a well-developed spine, and a moderately large transverse process on each side. Posteriorly are two

[1] It is held by some that the invertebral disc represents the intervertebra of some of the lower forms, but this is probably incorrect.

articular surfaces which overlap the anterior articular processes of the succeeding vertebra; and the two anterior articular processes are overlapped by the processes of the vertebra above. These articular processes are sometimes called zygapophyses. The ribs articulate with the side of the body, above the point where the centrum meets the arch, and a second articulation is with the transverse process.

The neck vertebræ, except the first two, differ from the typical dorsal vertebræ, mainly in having no separate ribs; but rudimentary ribs are present, fused with the body and the small transverse processes. These rudimentary ribs form, with the base of the arches, foramina, through which the vertebral artery passes, except in the case of the seventh. The rudimentary ribs are distinct only in early development, but in the egg-laying mammals these cervical ribs remain distinct till the animals are more than half grown, and in the therapsid reptiles the ribs remain quite distinct throughout life.

The first two vertebræ are unlike any others. The reason for this is that to allow of rotation of the head the centrum of the first vertebra—or atlas, as it is called—has become fused with the centrum of the second vertebra, or axis, and the arch of the atlas has become united with the hypocentrum or intervertebra that originally lay between the atlas and the occiput. The atlas might be described as a

cervical vertebra which had lost its centrum and formed a secondary substitute from an intervertebra; and the axis as a cervical vertebra which has two

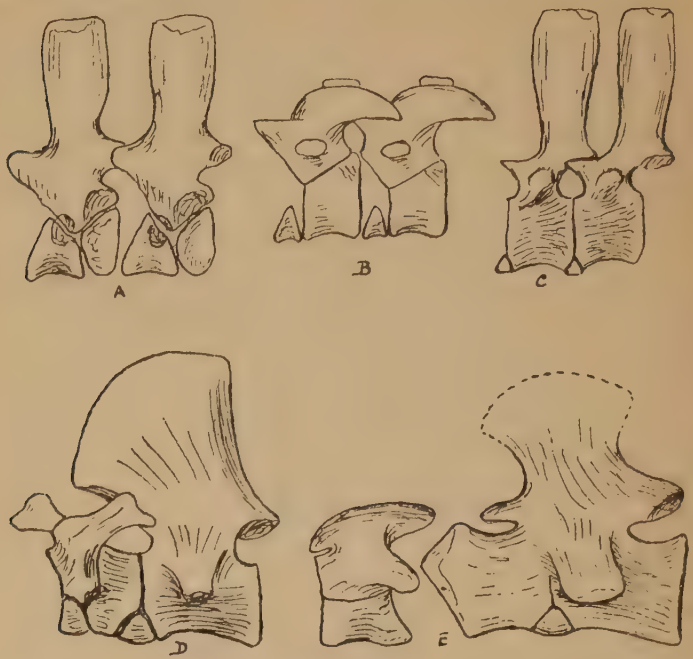


FIG. 33.—*A*. Two dorsal vertebræ of Labyrinthodont *Eryops*. *B*. Two dorsal vertebræ of higher embolomerous amphibian *Conodectes*. *C*. Two dorsal vertebræ of Theromorph *Ophiacodon*. After Williston. *D*. Atlas axis and proatlas of Theromorph *Ophiacodon*. After Williston. *E*. Atlas and axis of Dinocephalian *Jonkeria*.

centra, the anterior one projecting forward as the odontoid process.

The early structure of the atlas and axis is well seen in the theromorph and therapsid reptiles. In

these reptiles there are present two elements which are lost in the mammals—a pair of small elements in front of the arch of the atlas, the so-called proatlas, and an intervertebra between the true centrum of the axis, and the centrum which forms odontoid process.

In the lumbar vertebræ—the ribless vertebræ which succeed the dorsals—there are large transverse processes but no ribs. These transverse processes have never in man or most mammals separate centres of ossification, and thus cannot be regarded as ribs; but in the therapsid reptiles all the lumbar vertebræ have true, though short, ribs. Even in the wombat, and probably some other of the lower mammals, the lumbar transverse processes may also have autogenous centres of ossification, and be thus true ribs.

In the sacrum in man there are usually five vertebræ fused to form a firm support for the pelvis. In the first three there are developed below what are manifestly the transverse processes large independent costal elements, two at least of which articulate with the ilium.

In therapsids and mammals it is difficult to decide how many true sacral vertebræ there are, as the upper caudal vertebræ have independent costal elements not unlike those of the sacrals, and usually a number of these caudal vertebræ are fused with the true sacrals.

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Probably in man there are two true sacrals, and the other three vertebræ are really caudals which have fused with the true sacrals. In some mammals a very much larger number of caudals are united in the sacrum.

In most mammals there is developed a tail, and

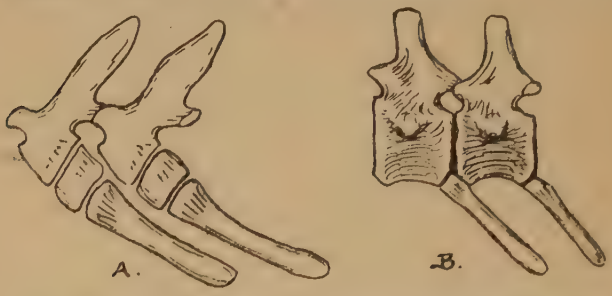

FIG. 34.—*A*. Two caudal vertebræ of Labyrinthodont *Eryops*. *B*. Two caudal vertebræ of Theromorph *Opkiacodon mirus*. After Williston.

in many of these chevrons are found. In man the tail is rudimentary, and is represented by the four rudimentary vertebræ that form the coccyx.

Sternum.—In all higher vertebrates with well-developed limbs the anterior dorsal ribs articulate in front with a median bone, or series of bones, which is called the sternum. The study of the early development of these sterna appears to show that they are formed by the fusion of paired elements which are developed on the ventral ends of the anterior ribs. Unfortunately one must at present say " appears," for the origin of the sternum is not

settled beyond question. We find in amphibians median elements in front which cannot have developed from ribs, since the ribs are often quite rudimentary. In the frog, for example, we have the well-known structures which go by the names omosternum, sternum and xiphisternum, which look as if they were in part at least homologous to the sternal structures of the higher forms. Whether they are, or not, has at present not been definitely settled. Certainly they are not costal structures. Just possibly, though the sterna in the higher forms appear to be costal developments, the appearances may be deceptive. Unfortunately palæontology does not help us much, as in nearly all early fossil amphibians and reptiles the sterna have remained cartilaginous, and have thus not been preserved as fossils.

The oldest-known ossified sternum is found in the primitive Permian two-arched reptile *Youngina*. Here the sternum has two plates lying behind the coracoids. Probably they were two ossifications in a large flat plate of cartilage. A few other reptiles have somewhat similar paired ossifications in the sternum.

In the mammal-like therapsids ossified sterna are known to occur only in the anomodonts and the gorgonopsians, and we can say with much confidence that the sternum was not ossified in either the therocephalians or the cynodonts.

In the anomodonts it is present as a rounded plate of bone, on which the posterior part of the interclavicle usually rests. In the semiaquatic *Lystrosaurus* the sternum is large and broad, and lies completely behind a very short interclavicle. Most probably it gives attachment to three ribs on each

FIG. 35.—*A.* Sternum of primitive Eosachian *Youngina*. *B.* Sternum of Anomodont *Lystrosaurus*. *C.* Sternum of Gorgonopsian *Lycænops*. *D.* Sternum of young *Echidna*. *E.* Sternum of man.

side, and certainly supports the coracoids in front. There has evidently been a cartilaginous extension behind.

In the gorgonopsians there is a fair-sized and well-ossified sternum. It gives attachment to the coracoids in front, and on its sides has attached to it certainly three, and probably four, ribs.

In the monotremes we meet for the first time with a segmented sternum. The anterior part is broad, and gives support to the coracoids and to the first ribs. This broad part corresponds to the anterior part of the human sternum, and is called the manubrium. In the young monotreme it is

seen to be composed of two halves, which unite in the adult. It is probably this manubrium alone that corresponds to the sterna of the anomodont and gorgonopsian. In most mammals and in man there are a series of segments behind the manubrium, usually four or five, which give attachment to a series of ribs, and these are followed by a small bone which has no ribs attached to it, except in front, called the xiphisternum.

CHAPTER VI

ANTERIOR LIMB

As has already been stated, there is good reason to believe that the limbs have been developed from lateral fins, but so far palæontological evidence has not given us all the steps by which a swimming fin has been converted into a walking limb. The lobe-finned fishes undoubtedly come nearest to the amphibians, but hitherto no fish has shown us a fin becoming a limb. *Sauripterus*, *Eusthenopteron* and the lung-fish *Ceratodus* have all fins that show what is manifestly the humerus, and the former two what are manifestly the radius and ulna, but we can only theorise as to how the walking limb arose. Wiedersheim and others have assumed that the tetrapod limb has been derived from the posterior part of an archipterygium such as is found in some sharks. Watson and others have held that the walking limb is derived from a fin such as we find in *Eusthenopteron*. The writer is of opinion that the front part of a fin such as we find in *Sauripterus* developed into a crawling limb, while the back part of the fin still for a time functioned as a swimming fin. The front part of the fin of *Sauripterus* was

probably used for scooping sand or mud, while the greater part of the fin was still a swimming organ. If we imagine a fin with the same elements as in

FIG. 36.—*A*. Skeleton of fin of lobe-finned fish *Sauripterus*. *B*. Possible condition of fin in a pre-Sauripterus type where front of fin is becoming a crawling hand.

Sauripterus, but without the scooping specialisation, we get a fin in which the anterior part might readily develop into a crawling limb while the back part still acted as a fin. With the further development of the anterior part into a walking limb the posterior part would rapidly disappear.

The shoulder girdle in the cartilaginous fishes consists of only a cartilaginous structure, but in the bony fishes there are in addition protecting bony elements in front. The primitive cartilaginous element was probably a plate whose upper side gave attachment to the dorsal extensor muscles of the limb and whose under side gave attachment to the flexors. In front were developed, in the early bony lobe-finned fishes, a median interclavicle, a clavicle and a cleithrum, with other bones above this last attaching the girdle to the back of the skull. As those latter are lost in the tetrapods we need not consider them. The cleithra, the clavicles and the interclavicle are retained in the well-developed amphibians, and in most of the mammal-like reptiles.

The cartilaginous element early developed a strong upward portion, which supports the limb to the cleithrum. This upper portion became the scapula of higher forms, and the most important of the cartilage elements.

It is unfortunate that in so many of the extinct forms we have only the bony parts preserved. In *Sauripterus* we have a large cleithrum, and doubtless a small clavicle and interclavicle. The cartilage bone element was evidently small, and probably consisted of only one ossified element—the scapula.

In the earliest known amphibians we have a

large scapula with the same three bony elements in front. Unfortunately the girdle is not very well known in any of the Carboniferous amphibians. In many of the Permian and Triassic amphibians it is fully known. There is a large median interclavicle,

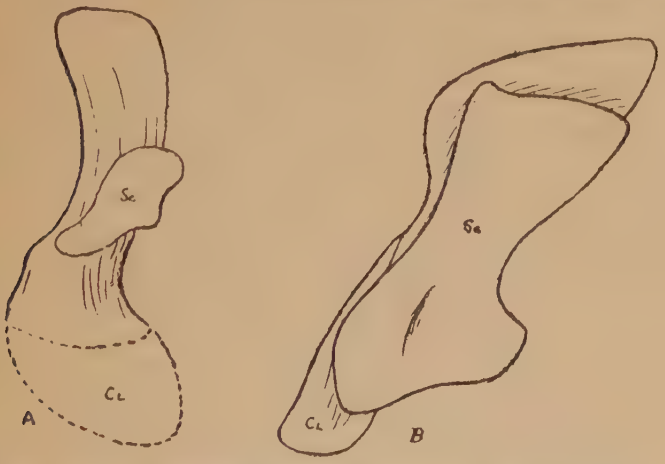

FIG. 37.—*A*. Shoulder girdle of lobe-finned fish *Sauripterus*. *B*. Shoulder girdle of Labyrinthodont *Cacops*.

with two large clavicles, the three together forming a sort of bony plastron. The clavicle sends a process up in front of the scapula. The cleithrum is a large bone which supports the greater part of the front of the scapula, and often its upper end as well.

There is usually only one ossified cartilage bone element, which is manifestly the scapula. In some forms there appears to be a distinct second element,

below and behind the glenoid cavity, in which hinges the humerus, and this element is doubtless the coracoid.

When we come to the primitive Permian reptiles we find the cartilage bone elements much better developed and the membrane bone elements reduced. The interclavicle is generally present as a T-shaped bone, and the two clavicles are relatively slender curved bones lying on the branches of the T. The cleithrum is a feeble bone in front of the top of the scapula.

The cartilage bone elements in those reptiles that lead on to the mammal-like reptiles are three in number. There is a large flattened scapula, with ventral to it two large elements, the posterior of which is the coracoid, and the anterior the precoracoid. In the precoracoid is a large precoracoid foramen.

Concerning the homologies of the ventral elements there has in the past been some confusion, and in many of the present-day text-books the confusion is continued. As will be shown presently, there cannot be the least doubt that it is the posterior of the two elements which is the true mammalian coracoid, while the anterior bone is very manifestly homologous with the anterior ventral element in the monotremes—sometimes called epicoracoid. As, however, the name "epicoracoid"

has been used for at least three different elements it seems best to accept the term "precoracoid," which has long been in use and is free from ambiguity.

The main source of confusion is, however, the fact that in the birds and most reptiles there is only

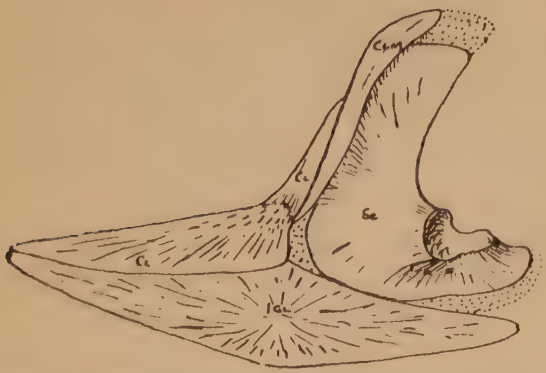

FIG. 38.—Half side view of left shoulder girdle of the Labyrinthodont *Lydekkerina huxleyi*. Natural size. The dotted areas are probably cartilage. The bony elements are figured in undisturbed natural position.

one ventral element, and there is little doubt that this is homologous not with the posterior but with the anterior ventral element of the mammal-like reptiles. This ventral element in birds, lizards and crocodiles has always been called the coracoid, and it certainly is a bit confusing to now discover that this is not the coracoid at all, but the precoracoid.

It is not known for certain whether the early

ancestors of the two arched reptiles had two ventral elements and lost the posterior, or whether in them there never was more than one ventral element. As, however, there are two ventral elements in the lizard-like anapsid reptile *Procolophon*, and also two in the very primitive lizard-like *Arœosceles*, we seem justified in concluding that the posterior element, or true coracoid, became reduced and was ultimately lost, and that the large bone that was left, and came to function as the coracoid, is really the precoracoid. In the theromorph *Varanosaurus* we find just such a change has taken place.

In the early mammal-like reptiles, such as the dinocephalians, the carnivorous therocephalians and gorgonopsians, and the small running dromasaurians, we find a moderately flat scapula and large flattened precoracoids and coracoids. There is always a large interclavicle and well-developed clavicles, and in the dinocephalians, therocephalians and gorgonopsians there are small cleithra, but not in the dromasaurians. There is no acromian process developed; and there is no ossified sternum except in the gorgonopsians.

In the more mammal-like anomodonts there is always a well-ossified sternum, and a great advance is seen in there being a large well-developed acromion process. This has doubtless arisen from a greater development of the supraspinatus muscle,

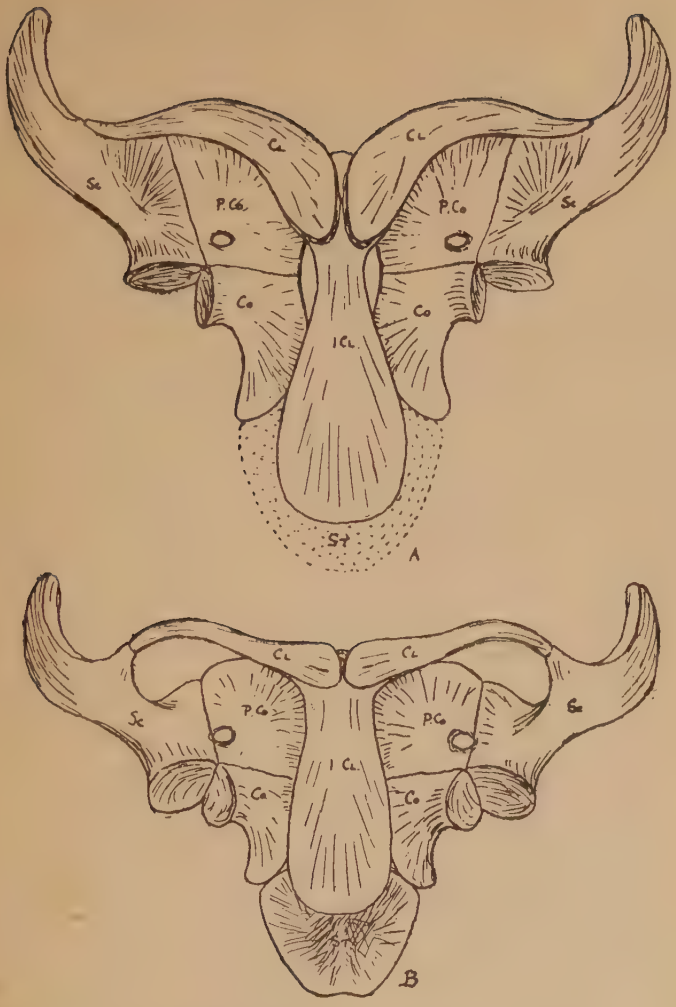

FIG. 39.—*A*. Shoulder girdle of Therocephalian *Pristerognathus*. *B*. Shoulder girdle of Anomodont Dicynodon.

which is, as it were, trying to work its way round the scapula. There still occurs a small cleithrum in front of the upper part of the scapula.

In the cynodonts the shoulder girdle has lost the cleithrum and the ventral elements are somewhat reduced. The acromion, though present, is less developed and mammal-like than in the anomodonts.

In the very mammal-like ictidosaurians the precoracoid no longer articulates with the scapula, and the girdle thus resembles that of the monotremes. There is a well-developed acromion process.

In the monotremes the girdle is essentially similar to that of the therapsids. There is, however, no cleithrum, and the precoracoid does not articulate with the scapula. The interclavicle is T-shaped, with the upper processes very long, and closely united to the rather feeble clavicles. The acromion is well developed.

The marsupials have in the adult condition a shoulder girdle essentially similar to that in most mammals and man. The scapula is large, and attached to the sternum by only a loose clavicle. It was thus until comparatively recently believed that the marsupial girdle differed very markedly from that of the monotreme. There were even those who maintained that the monotremes were descended from mammal-like reptiles but that the

marsupials and other mammals were not nearly related, and were descended from amphibians.

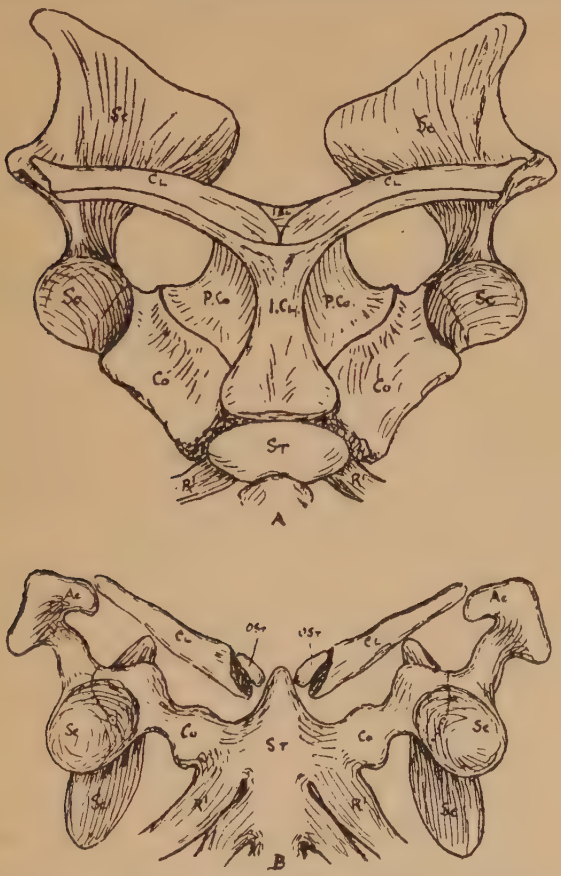

FIG. 40.—*A*. Shoulder girdle of a young *Echidna*. *B*. Shoulder girdle of newly born marsupial *Trichosurus*.

In 1895 I discovered, however, that in the very young marsupials the shoulder girdle is fixed to the

sternum almost exactly as in monotremes. At this stage the coraco-scapula is as yet unossified, and from the glenoid cavity the cartilage is continued uninterruptedly into the sternum. Part of this process becomes absorbed soon after birth, and the scapula, with its coracoid process, becomes free, as in the adult and in the higher mammals. As the coracoid process is clearly homologous with that of man, and it is this process which meets the sternum, it is manifest that it is the posterior element of the monotreme, and hence of the mammal-like reptiles, that is the true coracoid. The clavicles are early ossified, and before there is any cartilage in connection with them. This is of importance, since Gegenbaur has maintained that, as there are cartilage cells in the clavicle of the higher mammals, the clavicle is really grafted on the remains of the precoracoid. The study of the shoulder girdle in the therapsids, the monotremes and marsupials shows that the clavicle is a true membrane bone, with no trace of the precoracoid, and that the cartilage cells found in the clavicle of higher mammals are of no more morphological significance than the cartilage found at the angle of the jaw and on the coronoid process in many mammals.

At the inner ends of the clavicles of marsupials, and most higher mammals, including man, are small cartilage elements of doubtful significance.

Watson has suggested that these elements represent the remains of the interclavicle of lower forms, and this seems to be the most probable explanation. In man they are seen as the interarticular fibrocartilages. They are sometimes called the omosterna, but are probably not homologous with the structure called omosternum in the frog.

The spine of the scapula in man and the higher mammals divides the outer side of the scapula into two areas, the supraspinous and infraspinous fossæ. In the therapsids and monotremes there is no such spine. Some authorities have argued that the anterior border of the scapula in the monotreme corresponds to the spine in higher forms. But this seems to be incorrect. The anterior and posterior borders of the scapula in all the tetrapods are probably homologous. What has happened is that with the increased development of the supraspinatus muscle it has come to occupy a part of the outer surface of the scapula, and a spine has developed between the supra- and infra-spinatus muscles. In the very young marsupial there is no spine, and it develops as a ridge of membrane bone with no cartilaginous basis. In higher forms a cartilage spine develops.

The humerus in most of the early tetrapods is relatively short, and has a well-developed deltopectoral crest, and the distal end is much widened

to give attachment to the powerful muscles of the forearm. There is almost invariably a large entepicondylar foramen above the inner condyle, and usually an ectepicondylar notch or foramen. In all theromorph and therapsid reptiles the entepicondylar foramen for the brachial artery and the median nerve is still found, and in a large number of mammals it is still present. It no longer occurs in man, but occasionally a process of bone forms a deep notch which corresponds to it. An ectepicondylar foramen is present in many lower forms. It occurs in a few theromorphs and therapsids, but is unknown in any mammals.

The radius and ulna have varied very little during their evolution.

The carpus is known only in a very few of the early tetrapods, as it has generally been mainly cartilaginous, and it is thus at present impossible to trace the evolution through the amphibians. From the lower theromorphs right up to the mammals almost all details of the evolution are known. The carpus in the mammal-like reptiles consists of four proximal elements—the radiale, the intermedium, the ulnare and the pisiform—and either four or five distal carpals, with two centralia. This seems to be the common generalised type from which all reptilian carpi have been derived. The carpus is unknown in the Ictidosauria, but in the typical primitive

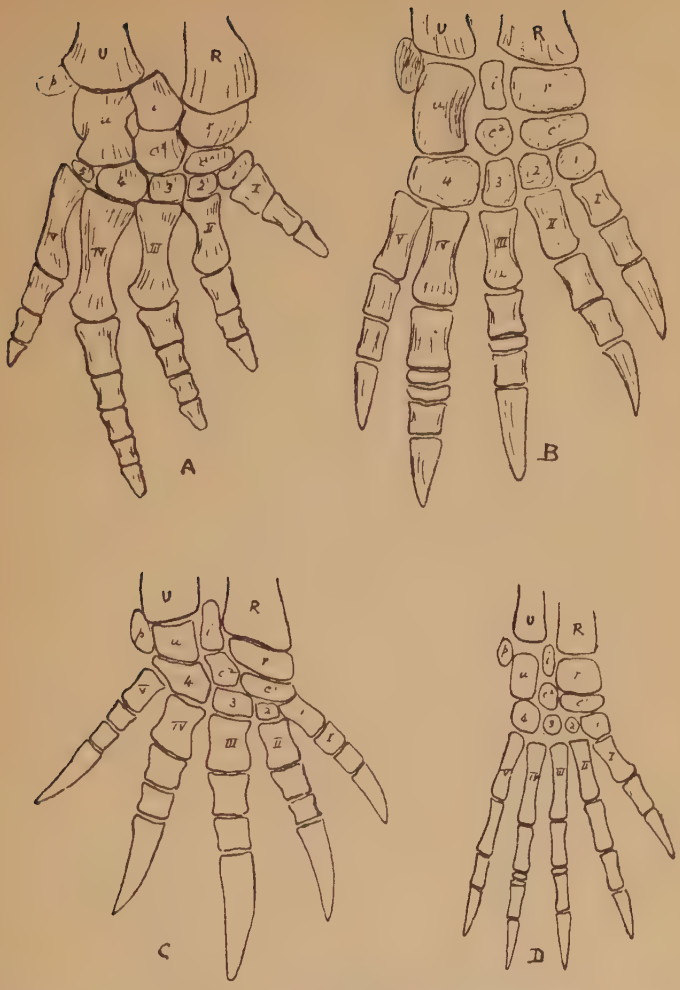

FIG. 41.—*A*. Manus of Theromorph *Ophiacodon*. After Williston. *B*. Manus of Gorgonopsian *Lycænops*. *C*. Manus of Anomodont *Emydopsis*. *D*. Manus of Cynodont *Thrinaxodon*.

mammals the carpus differs from that of the therapsid only in having lost the fifth distal carpal and the first radial centrale; and the fifth carpal is already lost in most of the mammal-like reptiles. In nearly all generalised mammals we have the four proximal and the four distal elements, with a centrale, and even in most of the primates we still have these nine. In the chimpanzee, the gorilla and man there are only eight, the centrale being lost. In man the centrale can be still detected in the early embryo, and it occasionally occurs in the adult as an abnormality.

The following are the names of the carpal elements used in text-books of human anatomy, with their comparative anatomy equivalents:

Os naviculare, or scaphoid = radiale.
Os lunatum, or semilunar = intermedium.
Os triquetrum, or cuneiform = ulnare.
Os pisiforme = pisiform.
Ossiculum centrale = 2nd centrale.
Os multangulum majus, or trapezium = 1st carpale.
Os multangulum minus, or trapezoid = 2nd carpale.
Os capitatum, or os magnum = 3rd carpale.
Os hamatum, or unciform = 4th carpale.

In each digit the first element is called the metacarpal and the more distal elements the phalanges. In the theromorphs and lower therapsids there are two phalanges in the first digit, three in the second,

four in the third, five in the fourth, and three in the fifth. These are the numbers not only of the mammalian ancestors but of most primitive reptiles. The digits increase steadily in length from the first to the fourth, apparently to bring the claws into line in the laterally placed feet. In the therapsids, where the feet come to be placed more beneath the body, the digits have to become more uniform in length, and this is effected by the reduction of one of the phalanges in the third toe and two in the fourth. In the gorgonopsian manus this is well seen. In the cynodonts the reduced phalanges are still less developed. In the anomodonts, the bauriamorphs and the dromasaurians the rudimentary phalanges are lost, and we thus have, as in all typical mammals and man, a digital formula of 2,3,3,3,3.

While in mammals, as in reptiles, the majority of the skeletal elements are preformed in cartilage, the mammal, apparently owing to its being less precocious in its development, has the elements less rapidly ossified; and as a result most of the elements have, in addition to the main centre of ossification, subsidiary centres, which ossify the more outlying portions or processes. These subsidiary centres are called epiphyses. For the most part they are of no morphological significance, though some are of importance to the surgeon. The humerus is mainly

ossified by one large centre, which becomes the shaft; but in the proximal end are two subsidiary centres which unite to form the large proximal

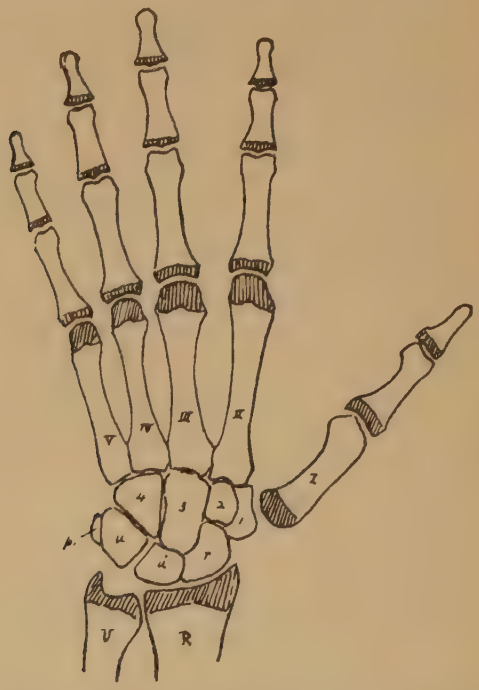

FIG. 42.—Hand of child showing the epiphyses.

epiphysis, and in the distal end of the humerus there are four more subsidiary centres.

So far as is known, there are no epiphyses at all in any of the elements of the mammal-like reptiles from which the mammals have sprung, every bone being apparently completely ossified from one centre.

As a rule, it may be stated that wherever for functional reasons any portion or process remains cartilaginous till late in development it ossifies from an epiphyseal centre.

In the hand of man a very remarkable arrangement of the epiphyses in the digits is found. The first metacarpal has a proximal, but no distal, epiphysis. All the other metacarpals have no proximal epiphyses, but distal ones. All the phalanges, on the other hand, have only proximal epiphyses. An explanation of this strange anomaly seems to be given us by the condition of the carpus in the anomodonts and some other therapsids. Here the first carpal is elongated, and apparently functions as a metacarpal, so that the main joint in the hand has been at the distal end of the metacarpals of the 2nd, 3rd, 4th and 5th digits, but at the proximal end of the first metacarpal in the case of the first digit. At these principal joints ossification was delayed, and epiphyses developed distally on the metacarpals and proximally on the first phalanges. As the metacarpal of the first digit was functionally a phalanx the epiphysis was formed on its proximal end. When, later, the first carpal again became reduced the first metacarpal also fell back, but retained its proximal epiphysis.

CHAPTER VII

POSTERIOR LIMB

The evolution of the posterior limb has most probably been fairly similar to that of the anterior, but unfortunately we know even less of the early evolution.

Most probably the earliest condition of the pelvis was merely a flat cartilaginous plate with the extensor muscles above and the flexors below, and this early plate we may consider as practically homologous with the pubis and ischium of the later types. When the fishes become walking or crawling tetrapods it became necessary for the pelvic plate to have further support, and the ilium developed as an upward plate, which, while supporting the limb, divided the extensor group of muscles into two lots.

Though the pubis and ischium were probably evolved before the ilium, the ilium early became the most important bone in the tetrapod pelvis, and appears to have been always ossified, while the pubis was of quite secondary importance. In many of the lower amphibians there are ossified in the pelvis only a large ilium and a large ischium.

In the later Permian amphibians and the earliest

known true reptiles there are a large pubis with a pubic foramen, a large ischium, and a relatively small ilium. The pubis and ischium unite with those of the opposite side by a long symphysis, and all four bones are moderately flat, this ventral portion of the primitive pelvis thus forming a large flat bony structure, and resulting in this type of pelvis being called "plate-like." A similar type of pelvis is found in the primitive two-arched reptiles, but the further evolution is quite different in the two great reptilian divisions. In the diapsida the pubis and ischium become elongated and diverge. But in the synapsida, or mammal-like group, the pubis and ischium always remain attached to each other, not only at their dorsal ends but at their ventral, and are never separated as we find in the dinosaurs, birds and lizards.

The pelvis is fully known in many of the theromorphs and in most of the therapsid orders and sub-orders. In the pelycosaurs, the therocephalians, the gorgonopsians and the dromasaurs the pubis and ischium remain of the plate-like type, and the ilium is small, and has a short iliac crest. In the dinocephalia the pelvis has become elongated, though the pubis and ischium still continue, as slightly modified only, from the plate-like type. In the anomodonts a great change has taken place. The ilium has become greatly developed antero-

posteriorly, and the pubis much shortened. The pubic foramen has become enlarged, and by extend-

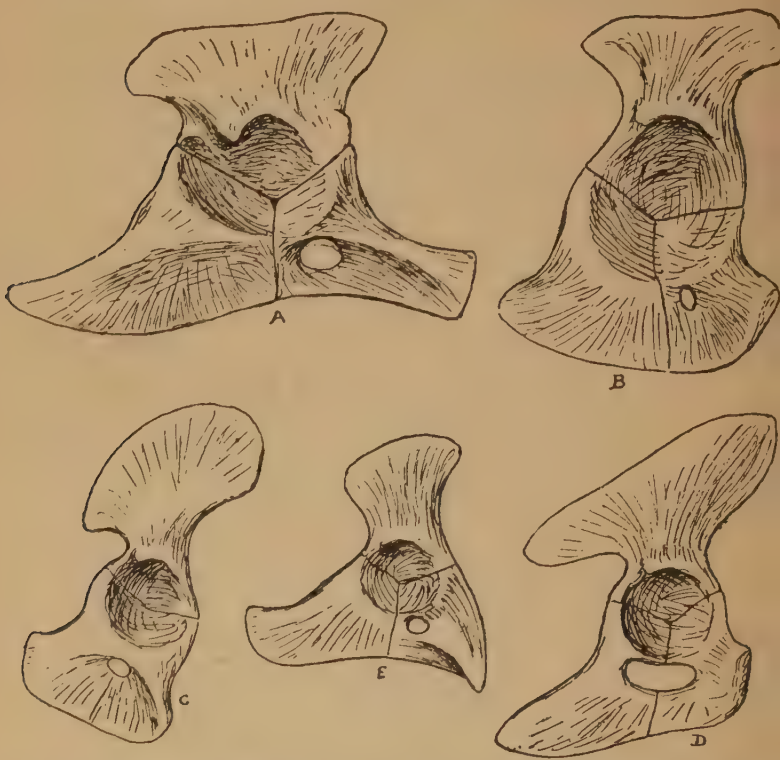

FIG. 43.—Bones of right side of pelvis in various Therapsids. *A*. Pelv bones of Gorgonopsian *Lycænops*. Reduced. *B*. Pelvic bones Dinocephalian *Tapinocephalus*. Greatly reduced. *C*. Pelvic bon of Anomodont *Emydopsis*. Nearly natural size. *D*. Pelvic bones Cynodont *Protacmon*. Reduced. *E*. Pelvic bones of Dromasauri *Galechirus*. About natural size.

ing to the pubo-ischial suture has become really a small obturator foramen. The whole pelvis has thus

become for the first time an approximation to that of the mammal. In the cynodonts the pelvis is still more mammal-like owing to there being usually quite a large obturator foramen. In some of the lower cynodonts there is apparently still merely a pubic foramen and no obturator; so that it would appear that an obturator foramen has been evolved at least twice independently. In both the anomodonts and the cynodonts the ilium passes forwards as in mammals, though also well backwards to a greater extent than in the majority of mammals. In some anomodonts, such as the semiaquatic *Lystrosaurus*, the ilium is greatly elongated anteroposteriorly, and is supported by as many as six sacral vertebræ.

In mammals the pelvis is only slightly modified from that in the cynodonts. The ilium is directed as much forward as, but much less backwards than, in the cynodonts; and in many mammals the ilium is reduced to a comparatively narrow bone. But though in many mammals the ilium is narrow, in man it is developed anteriorly and posteriorly nearly as greatly as in the cynodonts.

In the monotremes and marsupials there is developed in front of the pubis a bone called the marsupial bone, which supports the abdominal wall. It is unknown in the therapsid reptiles, though a homologous cartilage may have been

developed. It is not improbably the homologue of the prepubis formed in the pterodactyls, and possibly also of the prepubic cartilages found in many amphibians. As, however, no trace of a marsupial bone remains in any of the later mammals or man we need not further consider its homologies.

The femur has altered only slightly from the earliest known tetrapod femur to that found in man. There is a head, which articulates in the acetabulum, a long shaft and a pair of distal condyles. Near the upper end are a greater and a lesser trochanter; but while the position of the greater trochanter is fairly constant near the proximal end of the outer border, the position and development of the lesser trochanter varies greatly, according to the position which the femur usually occupied relative to the pelvis.

The tibia is nearly always in the tetrapods a well-developed and powerful bone. Its upper end articulates with the two condyles of the femur. Its distal end in the lower amphibians articulates apparently with the tibiale, but in the reptiles and mammals with a bone called the talus, or astragalus, whose affinities will be considered presently.

The fibula is almost always a more slender bone than the tibia. Proximally it articulates with the femur in the amphibia and reptiles and distally

with the calcaneum or os calcis, and generally also with the talus, or astragalus.

In the monotremes the fibula still articulates with the femur; and in most marsupials it articulates both with the tibia and femur. In the higher mammals the articulation with the femur is completely lost.

The evolution of the mammalian tarsus is still imperfectly known, and as a result very different interpretations have been given of the structures. Though, however, there are some blanks in our knowledge of the tarsus in the early tetrapods, all the stages of the evolution from the lower theromorphs to man are fully known.

In most amphibians the tarsus has remained largely or entirely cartilaginous, and it is only in a few of the extinct types that we know the full structure. Almost the only completely ossified tarsus known among the labyrinthodonts is that of *Trematops*, and this is probably a good example of the primitive amphibian type. There are three large elements in the proximal row, which may I think with confidence be regarded, as is done by Williston who first described this tarsus, as the tibiale, the intermedium, and the fibulare. Distally there are five tarsalia, and in the middle of the tarsus there are no fewer than four centralia.

In the somewhat later South African Upper

Permian labyrinthodont *Uranocentrodon* the tarsus is partly cartilaginous, but the ossified elements are found in undisturbed position in a number of specimens, and the restoration of the whole tarsus can be made with confidence. We find that the tarsus is strikingly similar to that of *Trematops*. It is interesting to observe that there is a canal between the two large proximal elements, and this canal can be seen between what are manifestly the homologous bones right up to man.

In the small fossil amphibian *Scincosaurus*, not at all nearly related to these labyrinthodonts, we have another type of tarsus, which differs mainly in having lost the centralia. There are, however, still three bones in the proximal row, and there can be no reasonable doubt that we are right in regarding these as the fibulare, the intermedium and the tibiale. The fibulare and the intermedium are certainly homologous with those of *Trematops* and *Uranocentrodon*. While the tibia articulates with the tibiale as in *Trematops* and apparently also in *Uranocentrodon*, it is the only bone that it does articulate with.

But if we are right in considering these two main bones of the proximal row of the tarsus as the fibulare and intermedium, then we must conclude that the two bones in the proximal part of the human tarsus—the calcaneum and talus, or os calcis

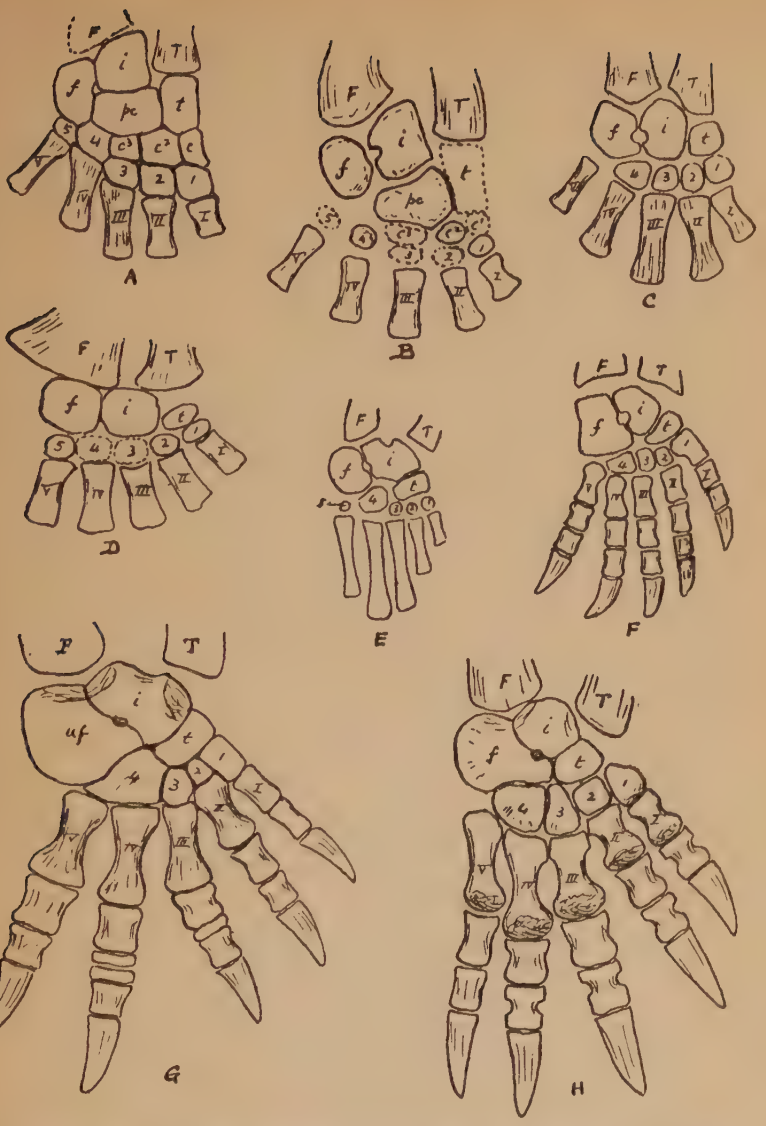

FIG. 44.—*A*. Pes of Labyrinthodont *Trematops*. After Williston. *B*. Pes of Labyrinthodont *Uranocentrodon*. *C*. Pes of amphibian *Scincosaurus*. After Jackel *D*. Pes of higher amphibian *Conodectes*. *E*. Pes of Anningiamorph *Galesphyrus* (?=*Annigia*). *F*. Pes of Anomodont *Emydopsis*. *G*. Pes of Gorgonopsian *Lycænops*. *H*. Pes of Therocephalian *Whaitsia*.

and astragalus—are also the fibulare and the intermedium. The only slight doubt that remains as to the evolution of the tarsus is the fate of the tibiale.

In the most primitive reptiles the fibulare and intermedium are always large and ossified, but the tibiale is frequently unossified or only partly ossified.

In the theromorphs the tarsus is known in a number of genera. The most primitive known is *Eumatthevia*. Here the fibulare and intermedium are very large, and the fibulare articulates with both. The tibiale is small, and situated between the intermedium and the first three tarsals. The tibia certainly articulates with the side of the intermedium, and it is just possible that the articulation may extend to the tibiale.

In the somewhat allied anningiamorph *Galesphyrus* the fibulare and intermedium are also large, and the tibiale of fair size. The fibula articulates with the two large elements, and the tibia mainly with the intermedium, but possibly also with tibiale.

In the typical therapsids the fibulare and intermedium are always large. In the therocephalian *Whaitsia* the tibia appears to articulate with the tibiale as well as the intermedium. There are four distal tarsals. In the gorgonopsian *Lycænops* the fibulare is much larger than in *Whaitsia*, and possibly acts as a heel. In the titanosuchia the huge

fibulare also seems to form a heel, and Watson informs me that a heel is formed by the fibulare in the cynodont *Diademodon* or allied genus.

In the Anomodontia the tibiale is frequently imperfectly ossified, but is a fairly large element in some forms. The tarsus is best known in *Emydopsis*. Here the fibulare and intermedium are large, with the usual canal between them, and the tibiale is quite as large as the intermedium, and it seems highly probable that the tibia articulates with it in part. The tarsus in the anomodont is interesting, further, in that the first tarsale is elongated, as is the first carpale, into a functional metatarsal.

In some of the primitive diapsid reptiles there is a tarsus very similar to that of the therapsids, and there then can be little doubt that the tibia articulates in part with the tibiale. In *Howesia* the tibiale is quite large, and in the living *Sphenodon* there seems no doubt that the part of the large fused proximal element that gives articulation to the tibia is really the tibiale.

In all typical mammals the tarsus is essentially similar to that in the therapsids. As the tibia is the main bone of the lower part of the leg the talus, or astragalus, becomes the main supporting bone of the foot. The calcaneum, or os calcis, is usually largely developed, to form a heel, and to give a strong leverage to the posterior muscles. The distal

bones of the tarsus are very constant throughout the mammalia, except where, as in ungulates, some of the toes become reduced or lost.

By many authorities it has been supposed that, while the calcaneum is the fibulare, the talus or astragalus is a fusion of the intermedium and the tibiale. The navicular is then held to be the centrale of the tarsus. But not only is there no evidence from palæontology or ontogeny of the talus or astragalus being a fusion of the intermedium and the tibiale, there is the most conclusive evidence that it is only a single element, and that this element is the intermedium. The only point on which there can be any doubt is whether the navicular is the tibiale or a centrale.

If the navicular is the centrale then the tibiale is completely lost. But the structure of the tarsus in *Scincosaurus* shows conclusively that, there at least, there was a tibiale and no centrale, and the same may be said of *Conodectes*. A few primitive types of tarsus have retained a centrale, but always with a tibiale in addition, and when one element is lost it seems always to be the centrale. We can thus, I think, be moderately certain that the navicular is merely the somewhat displaced tibiale.

The following are the names given to the tarsal bones in human anatomy, with the comparative anatomy equivalents:

Calcaneum, or os calcis = fibulare.
Talus, or astragalus = intermedium.
Navicular, or scaphoid = tibiale.
Internal, or 1st cuneiform = 1st tarsale.
Middle, or 2nd cuneiform = 2nd tarsale.
External, or 3rd cuneiform = 3rd tarsale.
Cuboid = 4th tarsale.

By a few authorities it has been held that the cuboid is a fusion of the 4th and 5th tarsalia, but this is certainly not the case. The 5th tarsale is last seen in the pelycosaurs and anningiamorphs, and is never met with in any reptile after Permian times.

The metatarsals and phalanges in the pes in the therapsids are strikingly parallel to the metacarpals and phalanges of the manus. In the therocephalians there is a digital formula of 2,3,3,3,3. In the gorgonopsians and cynodonts the formula is 2,3,4,5,3; with reduced phalanges in the third and fourth digits.

The epiphyses in the digits in the pes are arranged exactly as in the manus; and in the pes we find in many therapsids an elongated first tarsal functioning as a metatarsal.

In the mammals and man the whole pes has remained essentially similar to what we find in the therapsid.

CHAPTER VIII

HOMOLOGIES

It will be perfectly manifest that in a segmented animal like a vertebrate most of the segments are so closely similar to those which adjoin them that there is no difficulty in determining which parts are homologous; and it is interesting to try to trace the homologies even in those segments which appear to differ from the others.

In simple repeated structures like the vertebræ there are usually few difficulties in determining the homologies. Thus the centra of most of the vertebræ are manifestly homologous, and even in the atlas and axis there is little difficulty, as has been already shown, in explaining the peculiarities as due to the arch of the atlas having become detached from its centrum, and the centrum having become joined to the true centrum of the axis.

The rib homologies are also very manifest. The dorsal ribs are all very clearly homologous. In the cervical vertebræ small ribs have become joined with the transverse processes and the sides of the centra, and form with them the lateral foramina. In the lumbar region it has been pointed out that

the large transverse processes have taken the place of short ribs in the ancestors; and it is possible that, even though those processes have no separate centres of ossification, we ought to regard them as homologous with the ribs, the structures in the homologous regions being perhaps homologous though differently ossified. But this can be decided only when we know something of the modes of ossification of the vertebræ in the earlier mammals. At present we know nothing. The same difficulty is met with in the transverse processes of the caudal vertebræ in most mammals. Those regions are ossified by separate centres in the reptile ancestors, and there they are doubtless homologous with the true ribs. In mammals they are only very rarely ossified from distinct centres. In the sacrum the costal elements are undoubtedly homologous with the ribs. But again in the 4th and 5th sacral vertebræ we have lateral elements almost exactly similar to those of the 1st, 2nd and 3rd, but they have not as a rule distinct centres of ossification.

The intercentra when found are undoubtedly homologous, but in mammals the only ones remaining are those which form the lower part of the atlas and the chevrons of the tail, and of course in man there is only that of the atlas.

When we look at the skull we find an interesting problem, but one which is now mainly of historical

interest. The occiput looks exceedingly like a modified vertebra. There is the basioccipital with the notochord running through it in the early stage, and there are the exoccipitals which look like the two widened-out halves of the arch. And, if we conclude that the occipital segment is really a much modified vertebra, is it not possible that the whole skull is a series of greatly modified vertebræ?

This suggestion was made years ago by Goethe and by Oken, and it was worked out in great detail by Owen. Owen believed that the skull is really made up of four much modified vertebræ — the occipital, the parietal, the frontal and the nasal; and he made out such a strong case that, for ten years, almost everyone accepted his conclusions. Each of the four vertebræ had its centrum, its arch and its costal elements. The ribs of the 1st were the upper jaw; of the 2nd, the lower jaw; of the 3rd, the hyoid apparatus; and of the occipital vertebra, the shoulder girdle. And though the suggestion that the shoulder girdle is really the rib of the occipital seems to our modern minds very fantastic, we must remember that in the bony fishes the clavicular arch does articulate with the back of the skull.

Huxley showed, in 1858, however, that the facts of embryology are quite opposed to Owen's view of the skull, and that the shoulder girdle has really

nothing to do with the skull originally. And since that time Owen's theory has been completely abandoned by the scientific world.

Still, though Owen's theory had to be given up, there is an element of truth at the bottom of it. Embryology has shown that the head is really composed of a series of segments quite homologous with those which in the body give rise to the vertebræ, but there are many more than four, and they have little to do with the later developments of the bones of the skull.

Embryology shows that in the higher vertebrates the head is really composed of eight segments, but this early segmentation has had no effect on the ossification of the upper part of the skull. The gill arches are, however, clearly homologous with each other, and the hyoid, or second arch, is clearly also homologous with the arches of the gills. Then there is little doubt that the arch formed by the palato-pterygo-quadrate and mandible is also homologous. And thus we have quite a number of elements which as parts of homologous arches may be regarded as at least in part homologous.

The upper part of the first arch survives in the mammal as (1) the alitemporal or foundation of the alisphenoid bone; and (2) in the incus, which is the posterior part of the same element—the quadrate of the lower animals. The lower part of the first

arch is seen in Meckel's cartilage, the posterior part of which ossifies as the malleus.

In the second arch the upper part—the hyomandibular of the fishes — appears as the stapes in mammals. We can thus consider the alisphenoid and the incus as homologous with the stapes, the

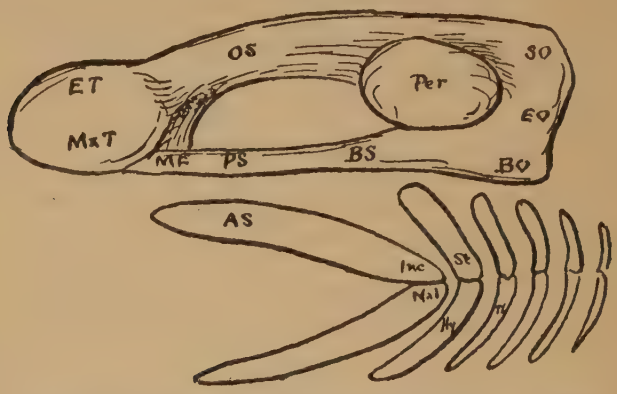

FIG. 45.—Diagram of cartilaginous skull of primitive vertebrate with the parts found as bones in mammals.

former two being developed from the upper part of the first arch, the latter from the upper part of the second arch.

The lower part of the second arch is found in the mammals as the hyoid bones.

In man the only ossifications that belong to this part of the second arch are the styloid process of the temporal bone, the body of the hyoid and the lesser cornu.

The third arch, or first branchial, is seen only in

the adults of the higher forms, as the posterior or greater cornu of the hyoid.

Formerly it was believed that the orbitosphenoid was homologous with the alisphenoid, the former being related to the presphenoid in the same way as the latter is to the basisphenoid. But the early development of the skull shows that the orbitosphenoid is really the same cartilage as that which joins the nasal capsule and the auditory capsule in the shark, and other fishes, while the alisphenoid is a development of the palato-pterygoid bar.

If we are right in believing that the fore and hind limbs are developments of anterior and posterior parts of a once continuous lateral-fin fold, and that each is developed from a similar number of segments, it would seem likely that we should be able to detect similar structures in the two limbs. And the digits of the two limbs are so similar, in detailed structure even, that it is hard to doubt that the limbs are homologous, though the homologies have been obscured in places by the different functions.

Omitting the membrane bones which were doubtless formed in connection with the operculum, we find three elements—the scapula, the precoracoid and the coracoid—usually present in early tetrapods. And in the pelvic girdle we have also three—the ilium, the pubis and the ischium. We have in the anterior limb a humerus, followed by two other

long bones, the radius and ulna. In the hind limb we have the femur, followed by the tibia and fibula.

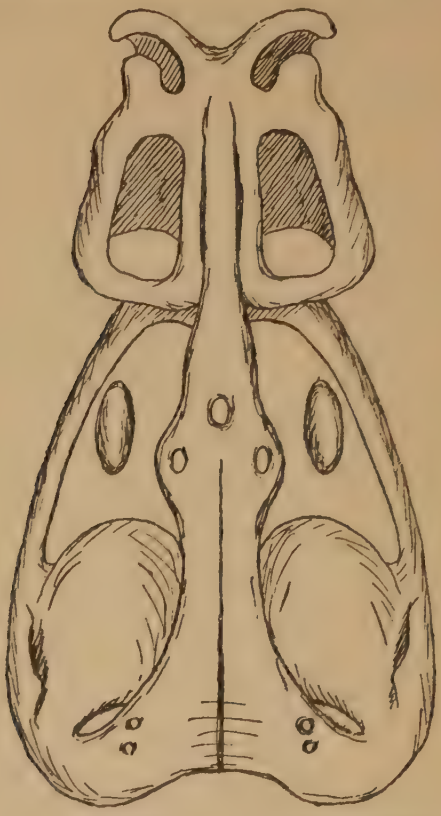

FIG. 46.—Cartilaginous skull of an embryo marsupial *Trichosurus*.

After the long bones we have in the one the carpus and five digits, and in the other the tarsus and five digits. As the limbs bud out in the same way we should expect the anterior border of the one to

correspond to the anterior border of the other, and the fact that the first digit of the upper limb with two phalanges lies in front, and in the hind limb the first digit with two phalanges also lies in front, seems to make the case very strong for a complete homology between the two limbs.

Assuming that there is this homology, the individual elements in mammals that correspond seem to be as follows:

Anterior Limb	*Posterior Limb*
Scapula	Ilium
Precoracoid	Pubis
Coracoid	Ischium
Humerus	Femur
(Not developed)	Patella (a sesamoid bone)
Radius	Tibia
Ulna	Fibula
Radiale	Tibiale
Intermedium	Intermedium
Ulnare	Fibulare
Pisiform (a sesamoid bone)	(Not developed)
Centrale	(Lost)
1st carpale	1st tarsale
2nd carpale	2nd tarsale
3rd carpale	3rd tarsale
4th carpale	4th tarsale

Anterior Limb—cont.	*Posterior Limb*—cont.
Pollex	Hallux
2nd digit	2nd digit
3rd digit	3rd digit
4th digit	4th digit
5th digit	5th digit

By some authorities an entirely different view is held of the homologies. It is believed by them that there is a reverse homology—that the anterior side of the front limb is homologous with the posterior side of the hind limb. The thumb of man is believed by them to be homologous with the little toe; the radius with the fibula, and so on. If mammals had been created without any ancestors, and the four limbs made to support the body as the four legs do a table, such a theory might seem probable. The knees go forward, the elbows backwards; and even the muscles seem to support the view that the legs are arranged round the centre of the body. But such an arrangement appears to be quite secondary, and the evolutionary history of the limbs from the early fishes seems to me entirely opposed to this reversed homology theory.

CHAPTER IX

EVOLUTION FACTORS

HAVING shown the principal stages by which the mammalian skeleton developed; how fins came into being; how they became converted into walking limbs; and how the first feeble cartilage skull became strengthened by bony plates and ultimately developed into the complicated bony skull we have in man; a little consideration might be given to the problem whether we can find any agency or agencies that may have brought about the changes. This is the great problem that has exercised all naturalists for more than a hundred years.

Various theories have been proposed; but we need consider only three, as most of the others are variations of one or other of these three.

A little over a hundred years ago Lamarck suggested a theory to account for evolution which has received a good deal of support. He had observed that if an organ is no longer used, or less used, by an animal that organ becomes reduced, or even lost; and that if a part or organ is greatly used it increases in size. This is known as "the law of use and disuse." He also held that the

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changes that are produced in an individual by use and disuse are transmitted to the next generation, or at least that they are to some degree inherited. This is called " the theory of the inheritance of acquired characters."

The difficulty of accounting for new organs, which of course could not be used till they have at least originated, he explained by the introduction of a psychic factor. He believed that where there is a new need this need initiates the new organ or part. In recent times the greatest supporter of Lamarckism has been Cope, the famous American palæontologist. His most important essays on the subject were published in 1887, under the very suggestive title *The Origin of the Fittest.*

In 1859 Darwin gave to the world, in his book *The Origin of Species*, another theory, which, supported by a great wealth of examples from the animal and vegetable kingdoms, gained the acceptance of most zoologists and botanists for over fifty years. The theory is, briefly, that in all animals and plants there are little variations, and that in the struggle for existence those forms with the more suitable variations survive and carry on the race. This has been called " the survival of the fittest."

Darwin himself, and many of his followers, believed, with Lamarck, that acquired variations are inherited, but many Darwinians not only held, and

hold, that natural selection of the fittest explains everything, but that acquired variations cannot be inherited.

If every species is subject to variations, and these variations are inherited, and nature selects the most suitable variations by killing off the less fit, then doubtless we have a theory that will explain much. But there are many difficulties. Most variations are comparatively small, and there is no evidence that these slight variations breed true. Then, though in many animals there is a considerable struggle for existence, it is very doubtful if very small variations are really matters of life and death. For example, if the protocone in the third molar of a zebra is a millimetre narrower than that of the average zebra will the possessor be more likely to die young? Or will a tiger whose canines are a millimetre shorter than the average be less likely to survive? Many structures are admittedly not helpful, and some of these are explained by what is really quite a different theory — sexual selection. The peacock's tail is believed to be the result of the female having an eye for beauty, and selecting as a partner the male with the most beautiful tail. What one sees in the habits of the barndoor fowl leads one to suspect that the female's powers of selection have been exaggerated.

Another difficulty, and a very serious one, is that

till an organ is really functional there is nothing to select. A new cusp on a tooth may be useful when once it functions, and selection might explain its further development, but till once it is functional it may even be a disadvantage. But perhaps the most fatal objection to Darwinism is that evolution has been progressive. A fish may evolve into a reptile or a mammal, but the reptile can only go back into an ichthyosaur or the mammal to a whale when there is a return to the old environment.

Though Darwinism is a most ingenious theory, and has been supported by some of the ablest naturalists of the last seventy years, there have always been those whom it failed to satisfy, and to-day the number of convinced Darwinians is very much smaller than forty years ago. Bateson, in his address to the British Association in 1914, said: "We go to Darwin for his incomparable collection of facts. But to us he speaks no more with philosophical authority. We read his scheme of evolution as we would that of Lucretius or of Lamarck, delighting in their simplicity and their courage." But Bateson has nothing to put in its place. Then the geneticists have shown that most minor variations, on which Darwin based his theory, are not inherited at all. They believe it is true that certain external agencies, such as heat, light, radium emanations, etc., can bring about changes in the

germplasm, and that such changes are inherited. But no such changes as the geneticists have so far been able to demonstrate throw the slightest light on evolution as the palæontologist sees it.

Watson, in his address as President of the Zoological Section of the British Association in 1929, expresses his dissatisfaction with both Lamarckism and Darwinism. "The only two theories of evolution," he says, "which have gained any general currency, those of Lamarck and Darwin, rest on a most insecure basis; the validity of the assumptions on which they rest has seldom been seriously examined."

Recently there has been some revival of the old idea that there is more in life than can be explained by physics, and even Lamarck, as has been said, invoked a psychic factor to account for the origin of new organs to meet the needs of an animal. And within the last twenty years two elaborate philosophical works have appeared which deal with the problems of evolution.

In Bergson's *Creative Evolution* we have a most fascinating discussion of what he believes to be a "vital impetus," which has directed evolution. And more recently we have the remarkable work of Smuts on *Holism and Evolution*. Smuts believes that throughout the universe, in the inorganic as well as in the organic world, there is something ever

tending to unite parts into wholes, and always bringing about higher types of organisation; and in the animal kingdom higher and higher forms, till we reach man.

This theory of Smuts resembles in some respects that of some of the older philosophers, who believed that in all life there is some underlying perfecting and co-ordinating principle, which has sometimes been called "entelechy." Even in Aristotle we find a somewhat similar belief.

One cannot conclude better than by a further quotation from Watson's address: "The present position of zoology is unsatisfactory; we know as surely as we ever shall that evolution has occurred, but we do not know how this evolution has been brought about."

When the Scientists have failed to give us a satisfactory explanation of evolution we feel driven to consult the Philosophers. It may be that no explanation hitherto given is sound. It may be that we shall never be able to realise what is behind evolution. But it does seem that there is a "something" that cannot be weighed by physics or analysed by chemistry.

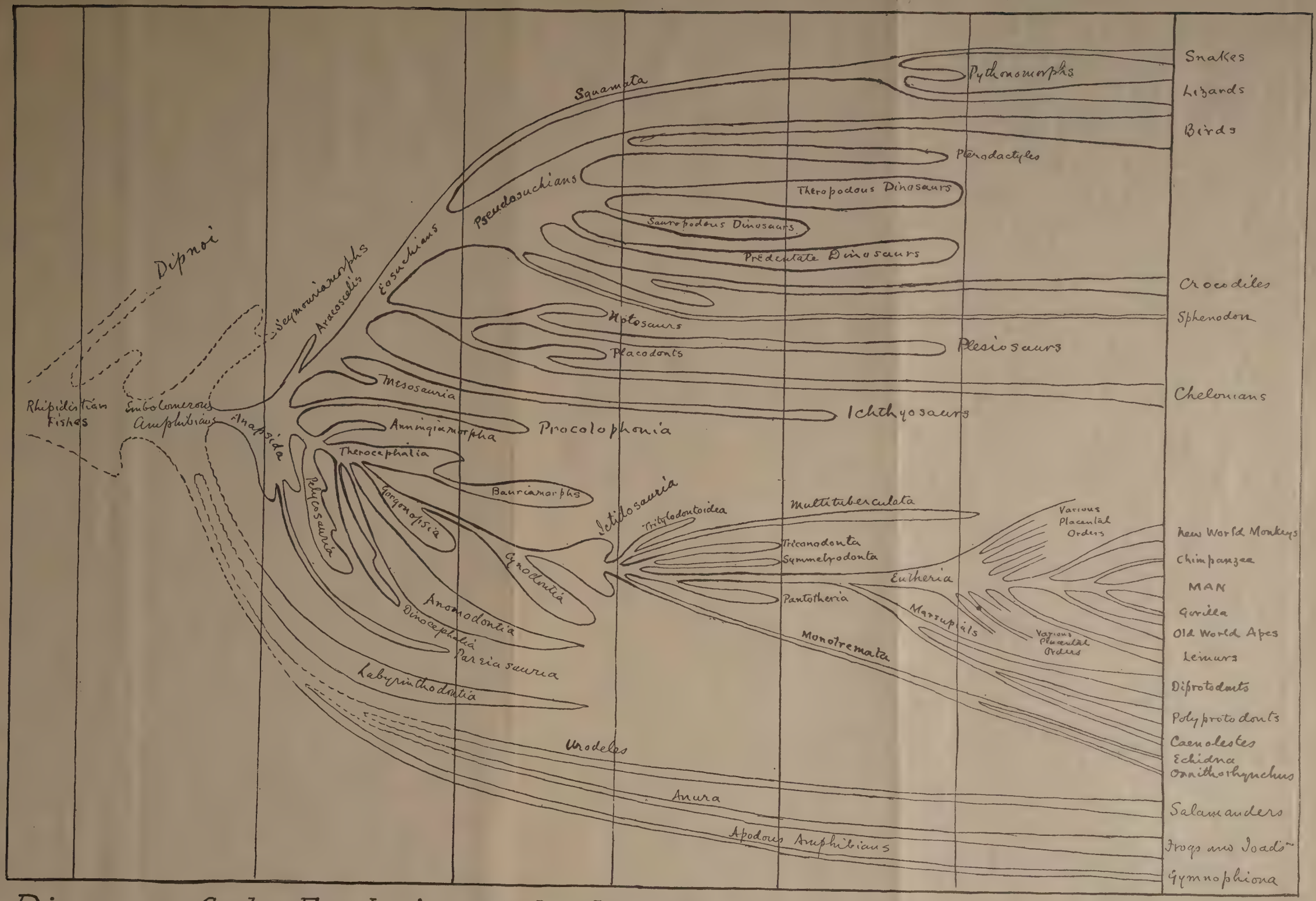
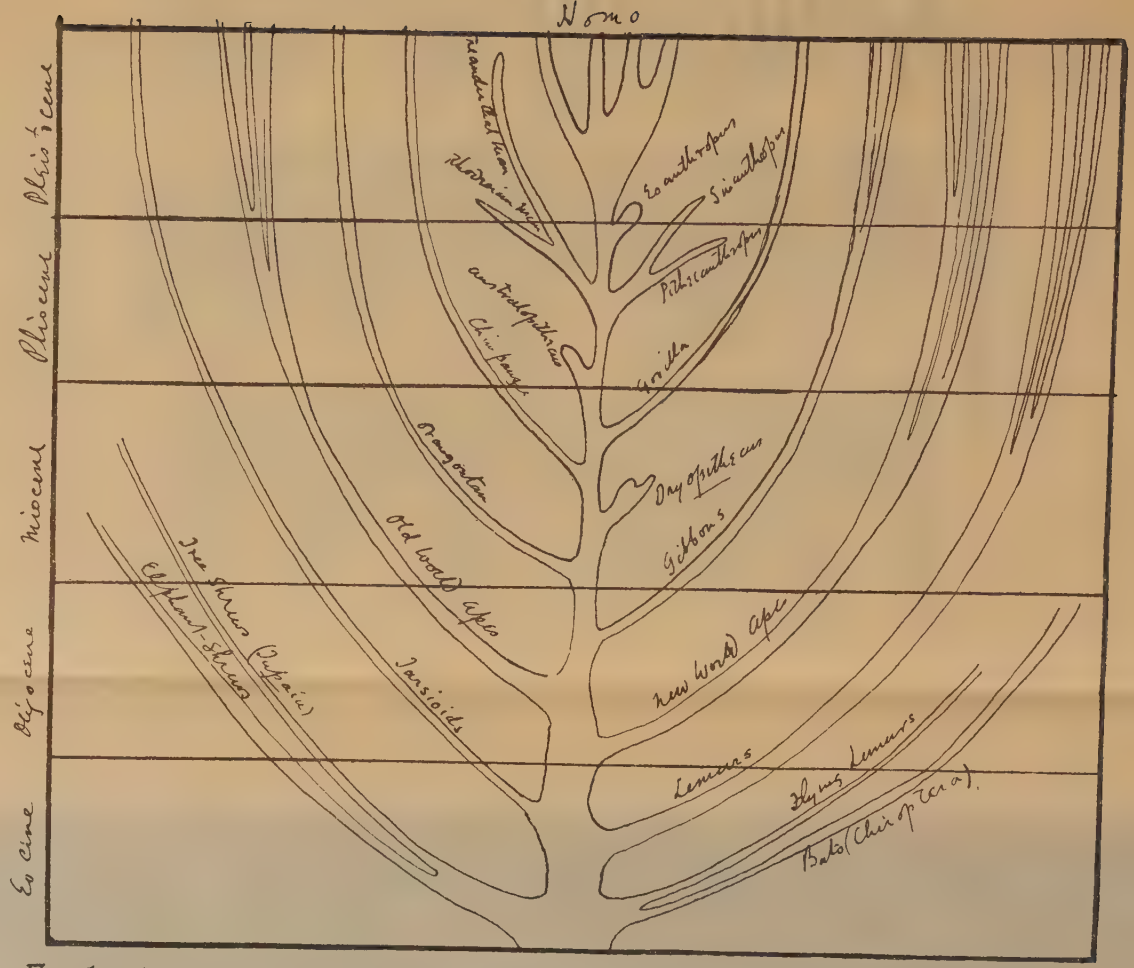


Diagram of the Evolution of the Amphibians, Reptiles, Birds, and Mammals.



Evolution of man and the apes from the beginning of the Eocene.

ABBREVIATIONS

A.C. Auditory Capsule
Ang. Angular
Art. Articular
A.S. Alisphenoid
B.H. Basihyal
B.O. Basioccipital
B.S. Basisphenoid
C^1, C^2. Centralia in carpus and tarsus
C.C. Carotid Canal
C.H. Ceratohyal
Cl. Clavicle
Clm. Cleithrum
Co. Coracoid (in views of shoulder girdles)
Co. Coronoid (in views of mandibles)
D. Dentary
E.O. Exoccipital
E.Pt. Epipterygoid
E.T. Ethmoturbinal
F. Fibula
f. Fibulare
Fr. Frontal
Hy. Hyoid
i. Intermedium
I.Cl. Interclavicle
I.Co. Intercoronoid
Inc. Incus
I.P. Interparietal
I.T. Intertemporal
Ju. Jugal
L. Lacrimal
Mal. Malleus
M.E. Mesethmoid
Mx. Maxilla
Mx.T. Maxillo-turbinal
Na. Nasal
N.C. Nasal Capsule
N.Cd. Notochord
O.O. Opisthotic or Paroccipital
O.S. Orbitosphenoid
O.St. Omosternum
p. Pisiform
Pa. Parietal
Pal. Palatine
P.Art. Prearticular
p.c. Proximal centrale
P.Co. Precoracoid
Per. Periotic
Pit. Pituitary Fossa
Pmx. Premaxilla
Po. Prootic
Po.F. Postfrontal
Po.O. Postorbital
P.P. Preparietal
Pr.F. Prefrontal
P.S. Presphenoid
P.Sp. Postsplenial
Pt. Pterygoid
P.Vo. Prevomer (Reptilian Vomer of most authors)
Q.J. Quadratojugal
Qu. Quadrate
R. Radius
r. Radiale
R^1. Rib (in shoulder-girdle figures)
S. Ang. Surangular
Sc. Scapula
Smx. Septomaxilla
S.O. Supraoccipital
Sp. Splenial
Sq. Squamosal
$S.R.^{1\ 2\ 3}$. Sacral Ribs
S.T. Supratemporal (in top views of skulls)
St. Stapes (in some views of base of skull)
St. Sternum (in views of shoulder girdles)
T. Tibia
t. Tibiale
Tb. Tabulare
Th. Thyroid
Th.H. Thyrohyal
T.P. Transpalatine
U. Ulna
u. Ulnare
Vo. Vomer
1 2 3 4. Distal Carpals and Tarsals

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